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A CASE OF POLYMORPHISM IN ASPLANCHNA SIMULATING A MUTATION

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DURING the fall of 1909 the writer accidentally discovered a case of heterogenesis in the genus *Asplanchna* which bore all the earmarks of a bona fide mutation. The two forms concerned were quite sufficiently different to be classed as distinct species, and even as strongly marked species. The transition was sudden and complete, without apparent intergradation. The transition was also in one direction only, and it could not be considered as in any sense due to an immediate cross, because the reproduction of the *Asplanchna*, aside from resting eggs, is wholly parthenogenetic.

Subsequent study of the same species, during the following spring, as it appeared in several different locations, supplemented by extensive experiments, showed that the phenomena in question were not those of typical mutation, but are rather to be classed as striking instances of polymorphism. As, however, their interest depends in large measure, for the writer at least, upon the ease with which they may be mistaken for mutation, I will first describe the facts as they appeared in the original collection of material.

This collection was made about October 1, in the remnant of a vile pool on the alkali flat west of the city

of Lincoln, Nebraska. This portion of the flat has for years been used as a dump, having been filled in several feet in depth mainly with compost. Two years previously a heavy summer flood had excavated a cavity, the size of a village lot, to the original alkali bottom, and in this cavity the pool remnant, to the depth of about one foot, remained. The water was dark brown with alkali and the essence of compost, but it suited *Asplanchna* exactly, for while almost no other plankton was present the *Asplanchnas* were so abundant as to almost touch one another; the sweep of a yard with a 20-inch dip-net brought up a double handful of the strained animals.

My original study was confined to material from this single collection because, a day or two later, a heavy rain flooded the pool, killing the *Asplanchna* to the last individual.

The collection in question contained two distinct types of *Asplanchna*. The dominant form, outnumbering the other several hundred to one, was of a large humped type, closely akin to *Asplanchna amphora*. I shall, however, postpone a detailed discussion of the species, as it is intricate, and unfortunately involves some controversy, while the interest in the phenomena which I wish to describe is not specially dependent upon it. Reference to Fig. 1 will show fairly well its general appearance, and I need but add at present that it was of very large size, frequently measuring 1,500 μ in length.

Sparsely distributed among the mass of these animals was a mammoth rotifer of related yet very different type. It was saccate, or, more truly, campanulate, in form. Its robust body, without humps, somewhat exceeded in length that of its more slender companion, while its enormous ciliated wreath or corona was extended beyond all limits that the writer ever expected to see in a rotifer. Its transverse diameter frequently equaled the entire length of the animal. This massive giant swam about with a typical though rather slow *Asplanchna* movement, vibrating or flapping first one portion and then another of the

ciliated corona in a very conspicuous fashion. When it met one of the other rotifers in a head-on collision it was much less inclined to contract or turn a quick somersault than was the companion type. As to the specific, varietal, or other classification of this large campanulate *Asplanchna* I could find nothing. I concluded that it must be an as yet undescribed species. Its distinctness was further borne out by the results of detailed study.

The characters hitherto most extensively used for specific definition in the genus *Asplanchna* are size, body form, type and development of nephridium, and the form of the trophi. As to the nephridia of the two forms in question, they proved, indeed, sufficiently different. Although built upon the same general type, their size and the number of flame cells bespoke wide separation. Rousselet, who is the first authority upon the classification of rotifers, in his last article[1] discussing the species of *Asplanchna* expresses his belief that the number of flame cells is constant in each species, although he admits that it is very difficult to make strictly accurate counts of these delicate organs. He assigns to *Asplanchna amphora* about 40 flame cells, and this is a much higher number than has hitherto been found in any other species. My preparations permitted much better counts than may be made on the living animal, but still I am not certain of exactness. I found, however, that even the humped rotifers frequently bore about 50 flame cells on a side, and in many instances I found 55. In the campanulate type the number was astonishingly greater. Not only was the nephridial tube bearing the tags longer, stretching from the knotted portion near the bladder in a wide diagonal curved line to the lateral edge of the corona, but it was very thickly studded throughout the greater portion of its length with the flame-bearing tags. The number was certainly variable in larger and smaller specimens, but it was frequently about 100, and in a

[1] "On the Specific Characters of *Asplanchna intermedia*," Hudson, *Jour. Queek. Mic. Club*, Second Series, Vol. VIII, pp. 7–12.

number of instances, by thoroughly conservative counts, I reached the surprising number of 115. The nephridial development in this giant rotifer is therefore in proportion to its large size and massive tissues. The trophi also proved sufficiently different and of a size hitherto quite unknown in the genus. A glance at Figs. 3 and 4, showing the trophi of the two types drawn to the same scale, will show at once their great difference. A detailed discussion of their minor features will show them to be still further apart.

In general, then, to judge by the structure of the females, the two types seemed very distinct, and several weeks of painstaking study, including the examination of several thousand individuals, left me with very little doubt that I was dealing with what we ordinarily class as distinct species.

It was while examining some of my first mounted slides of the large *Asplanchna* that I came suddenly on the evidence of apparent mutation. As is well known, the young of *Asplanchna* are highly developed before birth, and in the material which I was studying this chanced to be true to an unusual degree. My mounted slides, too, were perfectly transparent, giving views not only of all the organs of the adult, but of every organ and almost every histological detail in the structure of the unborn young. Examining these young, I noticed at first nothing peculiar; the young within the humped rotifers bore humps even more marked than those of the adult, it being one of the recognized characters of *A. amphora* that these body extensions reach a maximum development in the young at about the time of birth. The first young noted in the campanulate type were also, in all respects, essentially like the parents.

I was, therefore, astonished to suddenly hit upon a large campanulate rotifer containing an unborn rotifer, not of its own, but of the other, the humped type, Fig. 2. The word mutation was the first thing that framed itself in the midst of my inarticulate consciousness. But of

course I neither accepted at once the suggestion nor the apparent facts before me. Mutation, although among things proven, is among the things proven to be rare, and is therefore to be accepted in any given case only after fullest verification. Moreover, facts themselves are frequently deceiving. Perhaps the young humped *Asplanchna* did not belong within the body of its seeming parent. Perhaps it was some accidental inclusion forced through some invisible aperture in the side of the larger organism. In short, was it really in the uterus? Perhaps it had been swallowed by the adult campanulate and had managed afterward to tear its way through the digestive tract, which latter organ had then healed and allowed the prey to continue development in the body cavity.

While I was asking myself these questions and others, I was also assiduously seeking for more examples, for if the phenomena were regular more examples would certainly be found.

A number were indeed discovered, and every possible explanation was eliminated except that they were, as they appeared to be, young humped rotifers which were produced by normal parthenogenetic development within the giant campanulate type. I was able to discern, for some of them, that they were within the uterus, and in every way in normal position. The only slight sign of abnormality was that they usually seemed to be a little small for the parental organism producing them; they filled less of the body cavity than did corresponding young that were developed true to type. But upon second thought this was but one more sign of the completeness of the heterogenesis. These humped young were developing of exactly the size that they would have developed within the body of a humped parent; within the body of a campanulate they naturally left room, so to speak, to spare. The internal organs, too, of these heterogenetic young bore out, in detail, the conclusion suggested by the external appearance. The lighter

musculature, the narrower ovary- or shell-gland, were obviously characteristic of the smaller humped type. Most definite of all, however, was the evidence of the trophi. These are universally recognized as yielding characters of specific rank. They are wholly developed before birth, and they were very different in the two types in question. I used, therefore, the utmost pains to ascertain the nature of the trophi in these heterotypic young. The result was without question; the trophi in every case indicated a complete and sudden transition from the campanulate to the smaller humped type. This was true both in regard to size and in details of structure.

I concluded, then, after the study of every organ which I could make out with clearness in the material at my disposal, that these atypic young in the large campanulate *Asplanchna* represented, not an ordinary variation, but the sudden production of one type by another and quite distinct one.

But a number of questions suggested themselves at this point. In what number were these mutants, if such they really were, being produced? Was the production of one type by the other occurring in both directions, or only in the one in which I had chanced to find it? And, again, could transition specimens or any signs of gradation between the two types be found among the adults, or individuals of any age, in the material at hand?

As to the first question, I examined carefully 270 mounted adults of the giant campanulate type. Nearly all were in reproduction, but only 90 of them contained young sufficiently advanced in development and sufficiently well placed to allow a certain judgment as to their type. Of the 90 unborn young nearly one fourth (22) were indisputably of the humped type, while 68 were just as certainly of the parental or campanulate type. Nothing should be made here of the ratio of one fourth and three fourths. The phenomena in question are not the result of a cross, and, moreover, the determination hinges upon several factors; for one thing, upon my caution,

when dealing with the earlier embryos, in rejecting any case which was not quite certain. In other words, had I been working with live material and rearing the animals to a proper stage, a considerably larger proportion than one fourth would probably have turned out heterotypic.

To answer the second question—*i. e.*, whether this atypical reproduction were occurring in both directions or in one direction only—I first made a preliminary examination of several thousand individuals of the humped form, a high percentage of which contained well-developed embryos. I found no indication of any departure from normal reproduction. I then examined critically one thousand individuals, recording results in each case. Of this one thousand individuals, 419 contained young sufficiently developed and well placed to admit of safe determination. All were plainly of the parental type; nor did I find a single case in all this material that even suggested strong variation toward the larger humpless rotifer.

Transitional specimens, however, could, if present, be more certainly found among adults, or at least among individuals after birth. This was my third query. Did such exist? Throughout my entire examination I sought for them, but with little success. At certain stages in development each species approaches a little nearer to the other species. Thus the young of the larger, campanulate type are not only smaller, but have slightly bulging sides, suggesting the possibility of humps. Their corona, too, although very heavy and broad, is less disproportionately so than in the fully grown adult. But in no case was it difficult to determine the relationship of such specimens; other characters placed them at once, especially the enormous and differently formed trophi, which are fully developed before birth. Very old adults of the smaller humped type might possibly, at first glance, be taken for variants toward the larger form, in that their humps become smaller and less sharply marked off from the general body wall. In no other character, how-

ever, do they approach the campanulate type. Putting aside such stages, which, with a little practise, fall naturally into place, the amount of further variation did not prove to be great. The humps, both lateral and ventral, on the smaller type, did show a considerable amount of variation in relative size. And in numerous cases it was of interest to note that such variations were plainly hereditary; *i. e.*, an extra large female with, say, relatively small humps, would contain a large young individual that was obviously of the same type.

But these minor variations were to be expected; as well as their tendency toward transmission, but they had no evident connection with the type of change of which I was in search.

Of true transitional types I discovered but two possible instances. These two individuals were quite alike, but differed notably from any others of the thousands studied. Each was, all in all, indisputably a humped rotifer, but decidedly beyond the ordinary maximum size and with disproportionately small humps. The corona of each was much broader and its cells much heavier than in any other humped individuals observed; the body walls and musculature also were much heavier, taking the deep stain shown otherwise only by the campanulate. All of these characters approached more or less the campanulate type. Most striking, however, were the so-called ovaries. In each case they were of the heavy type shown by the larger rotifer. The nephridia did not admit of careful observation. The most crucial organ of all, however, the trophi, agreed wholly with the humped type in form, and, though large, did not exceed the maximum size found in the ordinary type. Studying these two individuals with care, I came at last to the conclusion that, although in a sense they might be called transitional, they were after all only variants of the humped type—variants pointing toward, but not actually leading to, the production of the campanulate type.

All in all, then, my search for signs of genetic rela-

tionship between the two types seemed to leave the evidence for mutation sharp and clear: the transition from the giant humpless *Asplanchna* to the smaller humped type was sudden and complete; it involved many characters; it was being effected in many individuals simultaneously; it was a transition in one direction only; intermediate types and fluctuating varieties seemed, in all the material studied, no more in evidence than was to be expected in any two species of one genus. At the close of this part of my study it seemed that I had found an ideal case of mutation, agreeing in every particular with the definitions of the concept put forward by its originator, DeVries.

However, just as I was finishing the study of the preserved material at hand, and deeming that I had reached the above conclusions with full certainty, I was suddenly halted by coming into possession of more living material, and material so surprising that my well-worked-out results again assumed the character of problems, and I resolved, if possible, to subject the whole to the test of experimental method and further observation.

It was about the middle of March, 1910, that the *Asplanchna* began hatching in a large covered aquarium jar in which I had placed some of the resting eggs the fall before. Between the last of March and the 10th of April the species also began to appear gradually in two ponds, in which, fortunately, the available food organisms for many weeks were wholly different. Observations were thus begun upon the species under diverse conditions, even from the start. And, as they were continued with but few and short interruptions through the spring, summer, and well into the succeeding fall,[2] the variety of conditions under which the development of the species was followed included very wide extremes. Thus, during a cold period in early April the species multiplied in shallow ponds upon which ice was forming nearly every

[2] Since the above was written nearly all of the phenomena recorded have again been observed during a second season.

night, while heavy prevailing north winds kept the water in continual turmoil. On the other hand, in July and August, I was able to study the species in both permanent and temporary ponds during periods of the hottest summer weather.

Side by side with these observations, and correlated with them as far as possible, a large number of culture experiments were carried out.

The general method was as follows: The ponds were visited several times a week, and such observations as possible made on the spot. Then large quantities of the animals, together with their food organisms, were brought to a basement laboratory and placed in large aquarium jars. These mass collections were sometimes obtained by merely dipping up the water and the organisms it contained in their natural degree of dispersion; at other times the organisms were much concentrated by the addition of large numbers taken with suitable nets. Few results were more interesting than the observation of the resulting phenomena in parallel aquaria in which the animals had been placed, now in small numbers, and again in various degrees of concentration up to almost actual contact.

The material in these mass cultures was critically examined and followed from day to day. Then, whenever interesting phenomena seemed to be occurring, either in the ponds or the mass cultures, or in both, isolation experiments were begun with single individuals, or with a definite number carefully selected and examined one by one.

To my satisfaction, the animals proved remarkably adapted to experimental treatment. They withstand a great variety of environmental influences, providing only that two conditions are rigidly met. In the first place, a copious food supply must be furnished; and second, the fluid medium (it may be saturated with such ingredients that one hardly speaks of it as water) in which the animals have developed must be left practically un-

changed. This latter condition limits the range of possible experiment, but I could not once succeed in getting *Asplanchna* to live and reproduce in any other than its native fluid;[3] even dilution of one fourth with water from some other source seemed in every case to preclude a successful culture. In nature, too, every rain which diluted to an appreciable extent the vile ponds in which this *Asplanchna* flourishes results in the death of the entire stock, which is only replaced by the hatching of new individuals from resting eggs.

As to food, many organisms were tried, and a number proved available. Best of all, for the smaller forms of the *Asplanchna, Paramecium* proves an ideal food. Other rotifers come next, of which I used especially *Hydatina* and *Brachionus;* while, surprising as it would appear, the crustacean, *Moina paradoxa,* although a large-sized member of its group, provides, under certain circumstances, an available food supply for this overgrown and voracious rotifer. The adult *Moinas* are not eaten, but young and even half-grown individuals may be regularly eaten by the mammoth campanulate form I have described. The humped rotifers ingest the crustacea with difficulty, but succeed in doing so at times to a considerable extent.

Omitting further reference to methods, and refraining from any attempt to describe the course of experiments, I will briefly give their results, prefacing only that I make no general statement which is not based on the outcome of at least ten separate experiments or as ample observations in nature, or on both.

The first of these results which I will state, although nearly the last that I demonstrated, is the error of my original conclusion in regard to the relationship betwen the two types already described. The campanulate and humped types do reproduce each other reciprocally, although with very different frequency in the two direc-

[3] This does not apply to cultures started from resting eggs. These may be hatched and the young developed in varied media.

tions. Moreover, transition forms (in every feature except the trophi) do occur between them under given though unusual conditions. The phenomena thus fall more naturally under the rubric of dimorphism than under that of mutation; although, as will be apparent later, the phenomena with this rotifer bring the two concepts into closer relation than they have perhaps ever been brought before.

The second general result of work with the living animals was the surprising discovery that the species is not only markedly dimorphic, but trimorphic, possessing a third form—a smaller saccate type which differs from both the humped and the campanulate types quite as much as these differ from each other, and which, curiously enough, differs far more, in external appearance at least, from these other forms of its own species, than it does from an allied but distinct species, *Asplanchna brightwelli.*

I shall return to this latter point of specific distinctness again. But by way of description I will here state that this saccate type, as I shall call it, although showing a considerable range of fluctuating variability, is a rather primitive but typical *Asplanchna.* In size it averages much smaller than either of the other types dealt with, reproductive individuals ranging from about 500μ to 1,200μ in length. In outward form it resembles closely, now *A. brightwelli,* now *A. priodonta.* The corona, when the animal is seen from the end, is always circular, as is typical for the genus, never showing the strong dorsoventral flattening which is the invariable condition in the humped and campanulate types. Correlated with this circular corona is the general cylindrical shape of the animal. When placed on a slide in a shallow drop of water these saccates characteristically rest on their sides instead of their dorsal or ventral surfaces as do both of the larger types. The trophi are of the same type as are those of the humped *Asplanchna,* except that they are a little smaller and proportionally a little more robust.

The internal organs are of the same general character, although more compact and filling more of the body space than in the two larger forms, two of them, however, being notably different in development.

First, the nephridia. I have not studied these in stained preparations as I have in the other types, but, using living material, I make out a decidedly variable number of flame cells; they range from as low as twenty to nearly forty. It is at least plain that the number averages much less than in the humped form, and but a fraction of that in the campanulate. The difference would seem to be plainly correlated with the general differences in the size of the organisms.

Singularly in contrast to the smaller nephridia is the development of the contractile vesicle or bladder. This is a small organ in both the humped and campanulate types, but in the much more diminutive saccates it becomes very much larger, filling, when expanded, a large part of the body cavity. I have examined considerable numbers from diverse sources and reared under different conditions, to make sure that this contrast was not accidental. I find no exceptions to it. Like the number of flame cells, this matter of size of the contractile organ, relative to that of the body, has been hitherto considered a specific difference.

A final peculiarity of the saccate type, although a variable one, is its tendency toward an excessively rapid rate of parthenogenetic reproduction; it is usually crowded with embryos. Four, five and six are frequent; sometimes I have counted nine; while in many individuals they are so closely packed that counting is out of the question. These numerous young are also frequently born at a disproportionately small size, even compared with the diminutive parent, thus still farther increasing the extremes of size which the species presents. It seems probable that this smaller and less developed type is itself, to some extent, a product of this rapid rate of multiplication. I have found it multiplying at a slower

rate—*i. e.*, producing but one or two embryos; but such instances were always due to degeneration or growth under unfavorable conditions. I may add by way of contrast that the humped form most typically produces but one young at a time. Thus, in the material of my original study, among one thousand individuals I found but sixteen showing the more or less simultaneous development of two embryos, and none showed more than two. The campanulates regularly develop several embryos at once, four and five being common numbers; but in their capacious bodies there is no overcrowding, and certainly no curtailment of nutrition.

As to the occurrence, the definite relationship, and the causes of the production of the three types of the species, I have ascertained most of the facts, though not all.

The saccate form is, I think, unquestionably the only form that emerges from the resting egg. In all cases—seven in number—in which I have examined temporary ponds within a few days after formation and found this rotifer just appearing, or in which I have caught the species evidently close to its first appearance, I have found either nothing but the saccate type, or numerous saccates, together with transitional and humped types. In the majority of these cases the saccates have been rapidly displaced by the humped type, which, in nature at least, very rarely reverts to the production of the smaller form. As soon as the species is in full swing, so to speak, countless numbers may be examined for weeks without a saccate occurring. All of these phenomena have been paralleled in my aquaria, and I have also repeatedly observed the birth of the humped type from the saccate parent. This is usually in instances where the high numbers of developing embryos in the saccate parent have given place to few or to but one. Usually, too, the parent is a rather large saccate and the humped young a rather small example of its type. But occasional instances have been noted where the humped young, a moment after birth or

as soon as it had assumed complete expansion, appeared fully a third larger than its saccate parent. The act of giving birth to such heterogenetic issue is a decidedly prolonged and painful process for a rotifer, very different from the ordinary, sudden expulsion, well known in *Asplanchna.*

Turning to the consideration of the actual cause of the transition from the saccate to the larger humped form, I have not discovered it definitely. The cessation of the rapid rate of reproduction, already spoken of, seems a partial proximate cause, though it itself I can not explain. It seems in part a mere matter of the number of generations following hatching from the resting egg. But a copious food supply and generally favorable conditions probably favor the change. In early spring the saccate form maintained itself for several weeks in a pond where, in July, after drying up and being refilled by rain, the saccate form began to produce the humped form sparingly within four days, and was very soon supplanted by it. In another pond of purer water and seemingly less well adapted to the species, the saccate form appeared scantily in early May, and struggled on sparingly for three weeks, feeding mainly upon the flocculent masses of blue-green alga, but somewhat upon *Brachionus;* it then disappeared entirely, having produced no form but its own so far as I could discover. Yet in isolation cultures from this same stock, when fed on *Paramecium,* I raised, after several generations, a number of rather small humped *Asplanchna.*

While I have seen little evidence, thus far, that either of the larger types give rise to the saccate form in nature, yet in two small cultures I have produced a population of from one hundred to several hundred small saccates by the degeneration of the humped stock. In one case the colony was a very old one and the degeneration possibly due to this fact; in the other it was plainly the result of diluting the culture medium with tap water. The small saccates, even when they had dwindled to a half dozen,

before total lapse, still bore developing embryos in their diminutive bodies.

The typical case of relationship, however, is, plainly, for a few generations of rapidly developing saccates to be succeeded, after a few transitional forms, by a continuous and ever-increasing population of the humped type.

As to the occurrence of the humped type, this is, practically, as just stated. Although never hatching from the resting egg, it soon supplants the smaller and earlier form and then continues to multiply, in favorable localities, until put an end to by drought, rain, or the exhaustion of the food supply. I do not believe that it can multiply indefinitely, however, for in even my largest aquarium jars, the species invariably seems to die out after several crescendos and decrescendos of development. The largest cultures have lasted about five months. That their death is not due to the accumulation of metabolic products in the unchanged water seems probable, because in one case a new generation hatched from resting eggs soon after the death of the first, and showed no signs of weakness, although growing in the same long-used medium.

The occurrence of the giant campanulate form is a totally different matter from that of the other two types. It never occurs alone. It never occurs in newly hatched cultures or young stocks.[4] It rarely occurs in great numbers, and never does it do so, so far as I have ascertained, in nature when feeding upon what may be called a normal food. On the other hand, in old stocks that have

[4] This holds good under all ordinary conditions. Since the above was written, the experiment has been made of hatching out hundreds or thousands of resting eggs in a very small space—*e. g.*, a three-oz. bottle, in almost pure tap water. The results of this experiment are very striking. Placed thus from the start almost without nutrition, a few of the more vigorous animals begin cannibalism at once, with the result of a very early appearance of both the humped and the campanulate types. In just what generation they thus appear is not known, but very probably in the second and third respectively. The development and saltation occur with but few individuals, the majority starving to death or serving for food only.

become numerous, I find this giant type invariably present. The original collection which I studied was about typical in this respect. I have not ascertained the exact proportion which the campanulates bear to the humped form in any given case, for experiment shows that it is capable of variation within wide limits; but I think that in nature they would rarely equal one to one hundred.[5]

What was the relation of these two types? Weeks of all but continuous work were necessary to decipher it. The fact that the two types were so frequently associated indicated probable connection, but did not demonstrate it; the fact that the campanulate always appeared only long after the development of the humped form was again suspicious, but proved nothing. Isolation cultures of the campanulates soon showed, as my mounted material had done, that they regularly produced not only their own type, but a considerable proportion of the humped type as well. But the reverse process is at least so rare that I have been as unable to find it among my living material, as I was among that which I had mounted. Scores of isolation cultures, begun with few or single individuals, fed on diverse types of food, and nearly all very successful, remained negative in result, with the exception of one of my very first attempts. I was trying out the rotifer, *Hydatina,* as a possible food for the humped *Asplanchna,* and placed half a dozen of the ordinary type in a watch-glass with many of the smaller rotifers. Soon, among the young produced, there appeared one that rapidly developed into the giant type; but subsequent trials, carried on as long as this special food supply lasted, were negative in results.

Over against these failures, however, a large number of my mass cultures yielded at once *all but* conclusive evidence that the larger type was somehow derived from the smaller. These cultures were started as follows:

[5] During the recent summer one pond in which the species developed copiously from spring to August showed at the latter period a much higher number—about one campanulate to 20 humped.

From the surface of a pond several feet in depth, and at a point several feet from the shore, a large quantity of the humped type were collected with a small net. This material and the entire pond, so far as my investigations had gone at this time, had shown none of the larger form, and the care with which the material was taken from the surface rendered it improbable that a resting egg of the larger form should contaminate it, the resting eggs of all these rotifers being heavy and sinking at once.[6] This material was placed in clean transparent jars of several liters, although beside each larger culture was usually placed a smaller one in a tall thin vessel which permitted careful scrutiny of the entire contents with a low-power lens. It was almost impossible to crowd the animals to the point of injury, though perhaps every other visible organism would die. Now in all of these crowded mass-cultures, whether large or small, whether fed, half-fed, or starved, the campanulate form made its appearance within at most a week. Sometimes a single individual, either young or fully developed, would first be discovered; more frequently a number would be present before noticed. But in every instance the sudden appearance of the large form was followed by its very rapid multiplication, coincident with a still more rapid diminution in numbers of the humped form. The latter were eaten up by the former, even adults of the humped type falling victims to the prodigious ingesting power of the campanulates. This all but complete displacement, in the course, say, of three weeks, of one form by the other, was a striking and almost astonishing spectacle. I have not observed it in nature, however crowded the species becomes in its natural situation. But in my culture dishes it was the regular occurrence in case the individuals became sufficiently numerous.

[6] It has later been ascertained that, under certain circumstances, some of the resting ova may again rise and float; in a windy pool, however, they would very soon be blown to the margin and lodged. Yet the force of the experiments cited is reduced.

The suggestion of cannibalism as the cause was thus all but conclusive; but I was able to press the proof one step farther. My isolation cultures, started with one or a few individuals, invariably failing, I decided to try cultures started with a larger number of individuals, each one of which was first subjected to examination under the microscope. 240 individuals were thus isolated and placed in a single stender dish, care being taken to reject any that deviated never so little from the normal humped type, especially as to extra size. In the rapidly multiplying culture thus started there appeared within a week several typical campanulates, and the whole subsequent course of the culture duplicated the developments which had taken place in the mass cultures already described. This is as near as I have come to actually observing the production, by the humped *Asplanchna*, of its larger humpless congener. I have not witnessed the birth of the one from the other or seen it in uteri. The demonstration of fact is, however, sufficiently complete, and the farther conclusion is sufficiently plain, viz., that the transition in this direction between the two types is a relatively rare one. Not every humped *Asplanchna* possesses the power, whether this depends upon size, ingestive reaction or digestive capacity, to produce the larger form. Indeed, this power would seem to reside in but very few individuals.

As soon as I had reached even the tentative conclusion that cannibalism must be the cause of this marked heterogenesis, I set about to determine, if possible, why this should be the case. Was there some magic in the cannibalistic diet as such? Was it merely a case of rich nutrition? Or was the result perhaps due to the mere size of the ingested food organisms?

Excessive feeding with most of the usual food organisms of the species was plainly without result. So long as the *Asplanchnas* were relatively few or greatly outnumbered by their food organisms they glutted themselves to repletion without unusual consequences in re-

production. Thus in the case of one pond, an algal-feeding *Brachionus* developed until it exceeded in numbers anything that I had ever before observed under similar conditions. The surface water was so filled with them that one observer pronounced it as thick as good tomato soup. In this medium the humped *Asplanchna* gorged itself during days of rapid multiplication. Every stomach was packed with the smaller rotifers; yet no change in type resulted. Finally the *Asplanchnas* literally ate up the *Brachionus,* but themselves disappeared a short time after this was accomplished without having produced any of the giants. Yet condensed material taken from this same source and placed in large culture dishes did produce the cannibals some time after the *Brachionus* had been devoured. It follows from this instance, as well as from a number of others equally conclusive, that mere feeding on the flesh of rotifers, so to speak, is not sufficient to cause the change.

The same proved true of over-feeding on *Paramecium* and several other protozoa that were greedily eaten.

I was the more surprised, therefore, to discover one other food organism, and one only, so far as my observations extend, which is fully competent to bring about the same result. It is the Daphnid-like crustacean, *Moina paradoxa.* It seems almost incredible that a rotifer should feed upon this robust entimostracan, even the young of which are born of a size which would seem beyond the utmost stretch of a rotiferean stomach. Moreover, this *Asplanchna* does not by any means invariably attack *Moina.* It may disappear, seemingly from starvation, in a pond where *Moina* is present and rapidly multiplying. This has also happened repeatedly in my cultures, and I have placed numbers of the young *Moinas* in watch-glasses together with the *Asplanchna* without having them eaten. Yet in other very similar cases the young *Moinas* are ingested by the *Asplanchnas*—by the humped form, and rarely by the larger saccates. The very youngest *Moinas* may even at times be ingested by

the smaller saccates. It seems probable that the vigor of the *Asplanchna* stock, and, I think, the period in the reproductive cycle (number of generations since the resting egg), have much to do with the refusal or attack of this oversized food organism. Be this as it may, however, the habit of eating the young *Moinas*, once started, seems to rapidly become fixed in not only the individual, but its progeny and the whole subsequent stock; although, weeks later, perhaps, this feeding reaction may again be lost, and the last rotifers starve to death in the presence of abundance of young *Moinas*. Such starving stocks may be again revived, when almost perished, by the supply of a smaller food organism.

Now the feeding upon this crustacean has, to all appearance, the same effect in bringing about the production of the large campanulate type as has cannibalism. I have not proven it with the same precision, but I have observed the transformation of mass cultures from the smaller to the larger type under circumstances that suggested the all but certain conclusion that *Moina*-feeding was the initial cause. I have also reared large numbers of the campanulates, for weeks at a time, by using the young *Moinas* as food. Under these circumstances the humped rotifers all but disappear from the cultures. A few always remain, because they are continually being produced, in minor numbers, by the campanulate type. But as very few of the humped young are able to acquire the habit of *Moina*-feeding, they starve to death without reproduction or fall victims to their mammoth progenitors.

In one instance, and one instance only, I have followed the transformation of the *Asplanchna* to its largest type, through *Moina*-feeding, in nature. The case interested me much, being very different from any other instance that I have followed, and showing to an astonishing degree the protean possibilities of the species. As usual, the first appearance of the species was in this instance by scattered individuals of the saccate form. Their food

consisted chiefly of *Brachionus* and *Hydatina*. These organisms were not numerous, however, and were exhausted just as the countless hordes of the young *Moinas* appeared. Under these circumstances a wholesale transition to *Moina*-feeding occurred, even while the *Asplanchna* was in its earlier phases of development. The smaller humped forms had just begun to appear when the *Moina*-feeding began, both by these humped individuals and by not a few of the larger saccates. The species became for a few days indescribably chaotic. So far as body form was concerned, transition stages could be found between every possible type and variation. This is the only instance in which I have found the saccate form giving rise to the campanulate without the humped intermediate, but it certainly did so to a considerable extent in this case. The outcome of *Moina*-feeding in this pond was the establishment, after about nine days, of a new equilibrium for the species. The giant campanulates had become in this instance, and this instance only, among my observations in nature, the preponderant type, reproducing their own form in the main, but also a few slender, long-humped individuals. Of these latter a very few managed to ingest the *Moinas* and to reproduce, while the majority showed empty, shrunken stomachs and no developing embryos. All traces of saccate and transitional forms had disappeared.

I will note, in passing, that the campanulate form which is produced by the *Moina*-feeding is not quite identical with that procured by cannibalism. The size reached is even a little larger, and the animals have the appearance of being even more powerful in general musculature; but the flaring corona never becomes quite so extreme; the animals never assume quite the bell-like form which the most majestic cannibals present.

(To be concluded)

HARDINESS IN SUCCESSIVE ALFALFA GENERATIONS

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IN 1908 Mr. Charles J. Brand, of the Department of Agriculture, inaugurated an experiment in alfalfa to determine, among other things, the relations that different strains of alfalfa have to the cold of severe winters. The writer aided in this investigation.

For this purpose 68 regional strains of alfalfa were assembled from the various alfalfa regions of the world, many of them being foreign in immediate origin. The alfalfas were planted in hill and drill rows, and during the season of 1908 the rows were thinned so that accurate countings could be made. There were in the neighborhood of 80 plants to each strain. The winter of 1908–09 was particularly severe to alfalfa, and as a consequence most of the strains were sadly deleted.[1]

Twelve of the 68 strains were entirely killed, no living plants remaining. Twenty-eight of the strains killed out over 90 per cent., and over 60 per cent. of the strains killed out over 80 per cent. There were but 3 of the 68 strains that killed out less than 10 per cent. The killing of the American alfalfas was severe as indicated by the fact that the 9 strains from Utah killed over 90 per cent., while the 3 Montana strains killed over 65 per cent.

The hardier strains were those of more recent foreign origin. Two strains of the Grimm alfalfa had an average killing of less than 5 per cent., thus being the hardiest in the nursery. Neglecting the 12 strains that killed out entirely, the average killing of the nursery amounted to 77.51 per cent., using each strain as a unit.

[1] Charles J. Brand and L. R. Waldron, "Cold Resistance of Alfalfa and Some Factors Influencing It," Bulletin 185, Bureau of Plant Industry, U. S. Department of Agriculture.

During the summer of 1909 the seed produced by the living plants was saved from each strain separately. In the spring of 1910 a sowing was made of the original seed that had sown the first nursery, which had been designated as nursery *A*. This sowing was known as series 201. In addition another sowing was made in 1910, known as series 202, from the seed collected from nursery *A* in 1909. This sowing was from seed secured from plants that had survived the severe winter of 1908–09. In addition a number of rows were sown with seed from nursery *A* plants, selfed during the summer of 1909.

This second experiment, carried on by the writer, consisted of a number of duplicate rows seeded (*a*) with seed from original geographical sources, and (*b*) rows seeded with daughter seed obtained from the plants surviving the winter of 1908–09. These two seedings comprised 112 150-foot rows, each row containing up to 150 plants. During the summer of 1910 the rows were thinned and accurate countings were made. In the spring of 1911, after growth was well started, a determination was made of the number of dead plants, and in addition the living plants were gauged as to their vigor, on a basis of 1 to 10, the best plants receiving the highest markings.

The data obtained indicated the apparent increase of hardiness among the different strains. A possible source of error was the effect of vicinism in nursery *A* in producing hardiness in the progeny plants constituting series 202. Limited space prevents presenting the evidence which would lead one to think that this error was slight in effect and probably nearly negligible.

Only a brief summary of the results can be presented in this article, a detailed account of which must be left to a future publication. In the first place, let us regard the comparative results of the winters of 1908–09 and 1910–11 upon the strains in nursery *A*, and upon those of series 201. These two sowings were from the same lot of seed, and had they been representative samples one

would have expected that they would have fared relatively the same in the two winters. Deviations that might appear could be charged to the differences of the two winters, as we may suppose that alfalfa becomes acclimated in different ways to different types of cold.

The relation of the killing of the plants in nursery *A* and in series 201 is presented in the correlation table of

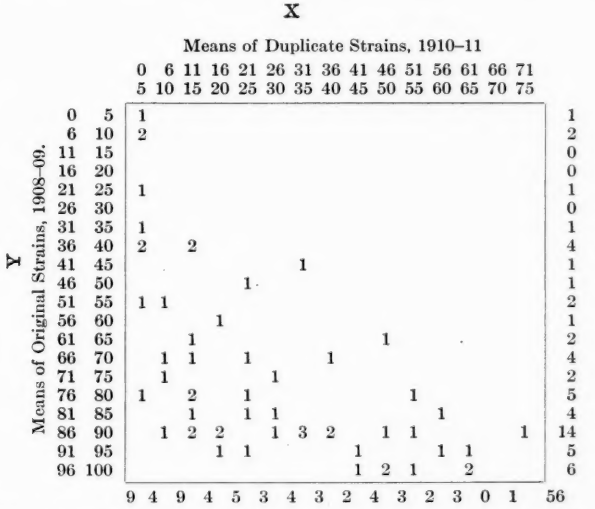

FIG. 1. Correlation of the means of various strains of alfalfa. Original nursery *A* seeding subject, duplicate of these strains in 201 series relative. Coefficient of correlation, $+0.62 \pm 0.06$. Standard deviation of *Y*, 24.85 ± 1.57. Standard deviation of *X*, 19.62 ± 1.24.

Fig. 1. The means of nursery *A* are the average per cents. of killing for the different strains, and the means of the duplicate seeding, series 201, are the corresponding per cents. for that nursery. In the table, the nursery *A* means appear as subject, and the means of series 201 appear as relative. The table shows good correlation amounting to $+0.62 \pm 0.06$, thus indicating that the two series of alfalfa were affected relatively the same by the two winters. This fact is perhaps more strikingly shown when the two series of means are platted on coordinate

paper. The ups and downs of one series correspond very closely with the ups and downs of the other series. The mean killing of series 201 was 27.43 ± 1.75 per cent. as against 77.51 ± 2.21 per cent. in nursery *A*, indicating that the second winter was the milder one.

The relation between the killing experienced by series 201 and series 202, during the 1910–11 winter, is expressed by the correlation table of Fig. 2. In this case the 201 series is subject and the 202 series is relative. The mean of the 202 series amounts to 6.43 ± 0.66. The correlation in the table amounts to $+0.46 \pm 0.07$. As

Y: Means of 201 Series	X: Means of 202 Series 0–5	6–10	11–15	16–20	21–25	26–30	31–35	
0–5	6	2	1					9
6–10	3	1						4
11–15	3	6						9
16–20	2		1	1				4
21–25	2		1	2				5
26–30	2	1						3
31–35	3	1						4
36–40		1			1	1		3
41–45	1			1				2
46–50	1	1		1			1	4
51–55		1	1		1			3
56–60		1		1				2
61–65	1	1		1				3
66–70								0
71–75					1			1
	24	16	4	7	3	1	1	56

FIG. 2. Correlation of the means of various strains of alfalfa. Duplicate seeding of nursery *A* (series 201) subject, progeny of the hardy plants of nursery *A* (series 202) relative. Coefficient of correlation, $+0.46 \pm 0.07$. Standard deviation of *Y*, 19.62 ± 1.24. Standard deviation of *X*, 7.35 ± 0.46.

indicated by the means of the two series, 27.43 and 6.43, there was a remarkable apparent increase in hardiness. This is partially expressed in the correlation table, but in the table the most pronounced changes do not work for a strong correlation.

For instance, one Utah strain killed out 59.6 per cent. in the 201 series, while its offspring killed but 6.2 per cent. in the 202 series. This indicates a weak correlation but a great increase in hardiness. There were but 3 instances of the 202 series killing more severely than the

201 series. Two of these instances were Turkestan alfalfas. The third one was due to the fact that the 202 row was an outer row, thus not afforded protection by an adjacent row.

In our theoretical discussion of the data we can scarcely more than present the problem. Within the limits of the pure *Medicago sativa,* as pure as it exists to-day, the fact is patent that there is a wide range of diversity in hardiness among the different strains of alfalfa, dependent in greatest measure upon their geographical origin. Strains of *Medicago sativa* that have been grown for long periods in cold climates, *e. g.,* Mongolian alfalfas, are found to be hardy during the severe winters of this country. Upon the other hand the strains of this species which have been grown for long periods in hot countries, *e. g.,* Arabia and Peru, were found to be exceedingly tender in cold districts. Thus at Dickinson, North Dakota, it has never been possible to bring alive through the winter a single plant of the Arabian alfalfas, and only under exceptionally favorable conditions has it been possible to winter any of the Peruvian alfalfa plants.

The diversity is so great between the Arabian and the Mongolian alfalfas that we must consider that hardiness has actually been added to the alfalfas which have become hardy, or that hardiness has been lost to alfalfas that have become tender.[2] It is not unlikely that changes have been brought about in both directions. The simple problem is, has this change come about through the "law of ancestral inheritance," or must the change be accounted for by distinct mutations occurring within any particular strain of alfalfa? Or is it possible that changes have come about through conformity to both methods?

[2] The fact is not lost sight of that an increase of hardiness may possibly be brought about by a recombination of certain (at present unknown) morphological characters physically responsible in different ways for the presumably complex character of hardiness. See Nilsson-Ehle, "Kreuzungsuntersuchungen," Lunds Univ. Ars., Bd. 5, Nr. 2, p. 114. Also a forthcoming article by the writer in the *American Breeders' Magazine.*

The belief that any strain of alfalfa is made up of many substrains with various steps of hardiness has been arrived at largely by *a priori* methods. We find that there are distinct morphological types of alfalfa within a strain which breed true, and that with other plants there are physiological types within any strain or variety likewise breeding true. It is reasonable to suppose that the same is true in regard to hardiness in alfalfa.

One of the Utah strains of the 201 series killed 42.8 per cent. from a total of 76 plants, and at the same time this strain of the 202 series sown from seed secured from three mother plants killed but 3.5 per cent. from a total of 131 plants. We have established at once a comparatively hardy alfalfa from one quite tender. With this Utah alfalfa, as with several others, it is difficult to avoid the conclusions that the strain is made up of many biotypes, relative to hardiness, which show their independent character even when no precaution is taken against interbreeding

We have also experimental evidence upon this point. Alfalfas that were selfed in 1909 were from both hardy and tender strains of alfalfa. A selfed Mexican plant had progeny that showed absolute hardiness during the winter of 1910–11, while the mother strain killed 24.5 per cent. Others of the selfed alfalfas acted in the same manner, producing offspring behaving radically different from the behavior of the parent strain. In some cases progenitors of non-hardy strains were selected from hardy strains.

It seems likely then that any regional strain of alfalfa as far as hardiness is concerned, is made up of biotypes with different cold resistant qualities. An alfalfa of this nature when moved to a colder region loses the representatives of the tender biotypes leaving the hardy ones for propagation. But this explanation accounts in no measure for the absolute changes of hardiness which some alfalfas must have undergone to have allowed the

species to accommodate itself to extreme climatic conditions.

While it is evident that there are alfalfas in existence to-day which do not contain elements of hardiness sufficient to allow them to live through the severer winters of the United States, this statement apparently does not hold for the alfalfas that are grown in the New World, with the exception perhaps of the alfalfa known as the Peruvian.[3]

Inasmuch as the South American alfalfas grown in hot regions contain elements capable of surviving very severe winters, it is apparently not necessary to assume recent mutative periods in the species. Inasmuch as the alfalfa plant grown in the New World contains elements of hardiness allowing it to persist through periods of severe cold, it is reasonable to assume that this element of extreme hardiness may be dissociated from the elements of lesser hardiness, even in the tenderest strains, in such a manner that it can be carried from generation to generation. This practical result has not yet been attained, not because such a result is theoretically impossible, but because no systematic attempt has been made. It is evidently a saner thing to commence practical breeding with those forms nearest to the one desired.

[3] Charles J. Brand, "Peruvian Alfalfa," Bulletin 118, Bureau of Plant Industry, U. S. Department of Agriculture. The Peruvian alfalfa is considered varietally distinct. This and the Arabian alfalfa have not as yet been found to possess elements capable of amelioration to the severe conditions of the north. Whether these two forms are retrograde mutants derived from the old alfalfa stock is impossible to determine at this time. One would be inclined to believe that such is the case.

The historically and long-continued growth of alfalfa in hot regions almost precludes the hypothesis of the loss of cold-resisting biotypes, which would obtain were the alfalfa strain transferred to a hotter region.

SOME FEATURES OF ORNAMENTATION IN FRESH-WATER FISHES

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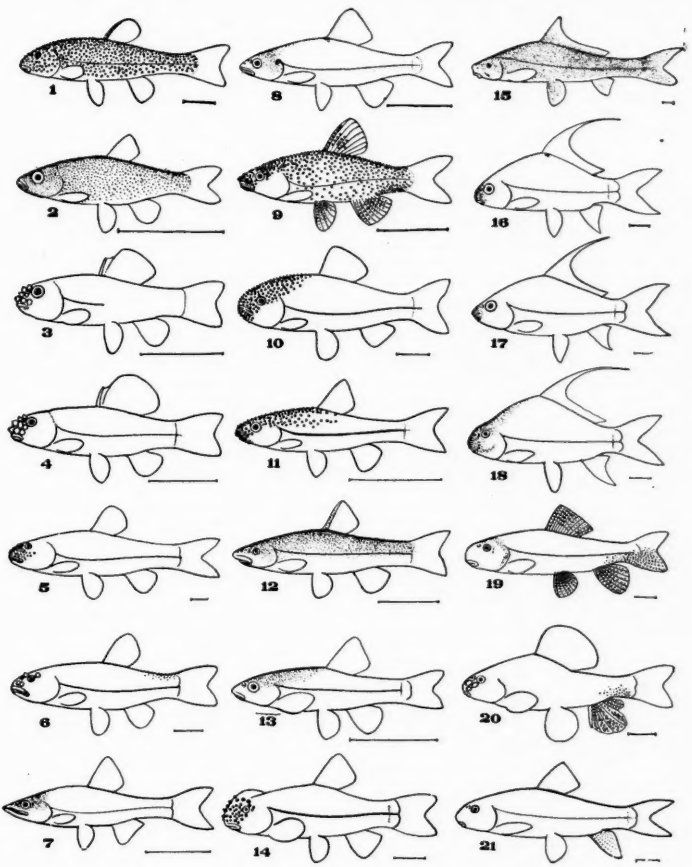
THE fishes known as the minnows (*Cyprinidæ*) and suckers (*Catostomidæ*) are familiar types to almost everybody. Certain of them during the spawning-season exhibit peculiar dermal excrescences or tubercles, these often rendering their appearance quite striking if contrasted with that of other seasons. These tubercles have long been known in many forms, though they do not seem to have been elaborately studied in connection with the relationships of the various groups in which they appear. Considerable difficulty may be encountered by those wishing to make studies of them, not only as they are seasonal and the fishes often difficult to secure at the required time, but also as they crumble and rub or drop off in alcoholic preparations, sometimes not even leaving the usual scars. It is hardly possible to arrange the distribution of the tubercles into distinctive groups of significance. Perhaps when enlarged and few in number on the head they contrast strongly with other cases, such as when very numerous and universally distributed. It may also be added that in a great many of the fishes belonging to the families under consideration no tubercles appear at any season, and this is often generic as well as specific.

As now understood the minnows embrace the largest family in ichthyology, having about 210 genera and 1,500 species in North America, Europe, Asia and Africa. They are mostly fishes of great similarity, small in size, weak, and among the most difficult in which to distinguish species. In this respect our local forms are very frequently no exception. Passing over the different genera



EXPLANATION OF PLATE

The figures are merely outlines, showing the distribution of the tubercles. All are drawn with the accompaning line representing an inch.

1. *Campostoma anomalum.*
2. *Chrosomus erythrogaster.*
3. *Pimephales promelas.*
4. *Pimephales notatus.*
5. *Semotilus bullaris.*
6. *Semotilus atromaculatus.*
7. *Leuciscus elongatus.*
8. *Leuciscus vandoisulus.*
9. *Notropis whipplii analostanus.*
10. *Notropis cornutus.*
11. *Notropis chalybæus.*
12. *Rhinichthys cataractæ.*
13. *Rhinichthys atronasus.*
14. *Hybopsis kentuckiensis.*
15. *Cycleptus elongatus.*
16. *Carpiodes difformis.*
17. *Carpiodes velifer.*
18. *Carpiodes cutisanserinus.*
19. *Catostomus commersonnii.*
20. *Erimyzon succetta oblongus.*
21. *Moxostoma macrolepidotum.*

and species from the Middle States region it has been my opportunity to study in the present connection, the following conditions are found.

The stone roller (*Campostoma anomalum*) occurs in the Mississippi Valley. In spring or early summer the adult males sometimes have the entire upper surface of the head and body covered with small tubercles, though on the fins I have only found them extending on the rudimentary dorsal rays. Though mostly attended with high coloration, red being more or less conspicuous at most of the bases of the fins, this is not always the case. Others were found full of spawn, without tubercles, but in high color.

The red-bellied dace (*Chrosomus erythrogaster*) is one of the most brilliant of all our common freshwater fishes, occurring mostly west of the Alleghanies. The adult spawning male has the entire head and body almost everywhere covered with minute tubercles in the greatest profusion. No females with tubercles have been secured.

The fat-heads (*Pimephales promelas* and *P. notatus*) are remarkable for their black heads, in the case of spring males, besides having only a few large conspicuous tubercles on the muzzle. The former species occurs only west of the Alleghanies while the latter is found in all the river-basins of Pennsylvania. The tuberculate males seem to be the exception, or of short duration in that condition, as among hundreds of examples of the latter but few were found.

The fall fish (*Semotilus bullaris*) and creek chub (*S. atromaculatus*) are two well-known fishes. The former occurs only east of the Alleghanies, and the fully adult male is with brilliant rosy sides and mostly rosy fins. Though reaching a length of nearly two feet, examples three inches long have been taken with fully developed eggs. The only tuberculated examples were all over a foot in length, and had only their muzzles densely covered with small tubercles. No nests were ever found made by the small fish of three or four inches in length.

The nests discovered were attended only by large fish. The creek chub occurs in most all our mountain brooks, and reaches a maximum length of ten inches, though males five inches long have tubercles. These tubercles are few, but quite conspicuous, and occur usually as a pair over each eye and one in front of the latter. Large examples have the scales on the hind part of the back thickened, or but slightly tuberculated. No tuberculated females of either species were secured.

The true dace (*Leuciscus elongatus* and *L. vandoisulus*) are represented by the former in streams west of the Alleghanies and by the latter in streams east of the Alleghanies. In both species the spring males have crimson sides and the top of the head minutely, but inconspicuously, tuberculate. In the eastern species occasionally a female will be found with tubercles on its head above, and also similar brilliant coloration to that of the male.

A few species of shiners (*Notropis*) present cases of tuberculated males. The silver fin (*N. whipplii analostanus*) of our eastern streams has the body and basal portions of the fin-rays largely covered with small tubercles in the adult male. The adult female is occasionally tuberculate. The red fin (*N. cornutus*), found in almost all of our streams, has the adult male very gaudy in spring, its tubercles appearing very conspicuously on the muzzle, front and predorsal region. Occasionally a tuberculate female is found. In the iron-colored shiner (*N. chalybæus*), often brilliant in the spring, the males sometimes have the muzzle, front and predorsal with many rather large tubercles. No females with tubercles were found.

The male of the long-nosed dace (*Rhinichthys cataractæ*) when fully adult has its snout, top of head, entire back and rudimentary dorsal rays minutely tuberculate in the spring. The adult male of the black-nosed dace (*R. atronasus*), one of our most abundant fishes, has the front and predorsal region minutely tuberculate in spring

and early summer. No tuberculate females of either species have been found.

The crested chub (*Hybopsis kentuckiensis*) is remarkable for the adipose-like frontal crest of the adult male in the spring, somewhat suggestive of the hooded seal. This species reaches ten inches in length, and examples half that size were taken with tuberculate muzzles, though without the crest.

The suckers are represented by 14 genera and about 77 species, mostly in North America, though several occur in eastern Asia. The following notes will show the conditions in those I have examined.

The carp-suckers (*Carpiodes*) occur in our waters mostly west of the Alleghanies. In several species (*C. difformis, C. velifer* and *C. cutisanserinus*) all have tuberculated muzzles or snouts in the spring males. In fact the last of these was so named by Cope for the fanciful resemblance of this very character to "goose-flesh."

The black horse (*Cycleptus elongatus*) has the body finely tuberculated over its entire upper surface in the spring. The upper surfaces of the paired fins are also tuberculated. Only large or old examples were examined.

Our common fine-scaled sucker (*Catostomus commersonnii*) is the only one of its genus east of the Alleghanies I have found tuberculate. It occurs all over our Middle Atlantic States. The tubercles appear within a very great range of age. Examples three inches long were found with well developed milt and roe, like those nearly two feet in length. The smallest examples with tubercles, which were only on the lower caudal peduncle surface, lower caudal lobe and anal fin, were four inches long. Others, nearly of the maximum size attained by the species, were found with exactly the same arrangement of the tubercles. Examples with the entire upper surface of the body and head, besides the dorsal and paired fins tuberculated, were always over a foot in

length, though seldom more. Further, I have every reason to believe these small fish were also spawning with the large ones, as I captured specimens of similar disparity in the same waters in the spawning-season. That many males spawn without ornamentation also appears likely. No tuberculated females were found.

The chub sucker (*Erimyzon sucetta oblongus*) has quite pronounced sexual differences, the spring males showing usually three large tubercles on each side of the snout, the anal rays tuberculated, and usually the last rays more or less incised. These characters only appear in males over five inches, and until the maximum size (eleven inches) is obtained.

The red horse (*Moxostoma*), with its numerous species, often exhibits the anal fin tuberculated (*M. macrolepidotum*). I have not obtained recent material, however, for these studies.

In conclusion the following may be stated.

First. The disposition of the tubercles in the ornamentation of breeding males is not always complete in the known design sometimes attained by certain individuals.

Second. The development of the tubercles may obtain in comparatively small or young individuals provided they are sexually mature. Tubercles occur, so far as I have observed, in the very young, especially in those species which undergo considerable transformation in certain apparent generalized characters, such as the development of the lateral line, change in coloration from a banded or spotted color-pattern to a more uniform tint, etc.

Third. The tubercles are subject to individual characteristics in being retained or lost for a greater or shorter period after the spawning season.

Fourth. The adult male alone in most species exhibits the tubercles, and though occasionally also present in the female of some species the latter seldom assumes equal development in other respects, such as bright pigment, etc.

Fifth. Sexually mature fishes spawn without the tubercles appearing, and in some cases frequently.

Sixth. The effect of different waters, like those of the sluggish warm lowland cedar-swamps where dark and blackish, as contrasted with clear cold rapid upland streams, does not seem to materially change the degree of development.

Seventh. Many species have the inner pectoral rays furnished with tubercles, and these no doubt are of assistance to the males in clasping the females during the spawning operations.[1]

[1] For the spawning in detail of some species see Reighard, in *Science*, XVII, April 3, 1903, p. 531, and Bull. Bur. Fisheries, XXVIII, 1908, pp. 1111–1136, Pls. 94–120.

THE FORMATION OF CONDENSED CORRELATION TABLES WHEN THE NUMBER OF COMBINATIONS IS LARGE

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AFTER the principles of any method of research are laid down by those who have the genius or the good fortune to make fundamentally new contributions, there always remains much to be done in the refinement, simplification, or adaptation of methods to render them most practically applicable in the routine of investigation. This is especially true in the modern higher statistics, where, at the very best, the labor is excessive.

One of the most onerous of the statistical processes is the determination of correlation in cases in which each individual measurement must be weighted by comparison with a series of others. In an earlier number of this journal[1] a method was described for the rapid formation of the heavy intra-class and inter-class[2] correlation and contingency surfaces by the use of a machine permitting simultaneous multiplication and summation. Methods of dealing with such correlations without the formation of tables will be published later. But abstract formulæ in the hands of inexperienced calculators are apt to lead to erroneous constants, which in the absence of the original data can never be corrected. Again, the validity of the correlation coefficient as a measure of interdependence depends largely upon linearity of regression. Hence, tables should be given whenever possible. The purpose of this note is to show how, in the case of relationships

[1] "On the Formation of Correlation and Contingency Tables when the Number of Combinations is Large," AMER. NAT., Vol. 45, pp. 566–571, 1911.

[2] These terms will be clear from their context in this note; they will be more precisely defined later.

involving a very large number of combinations, the chief advantages of the correlation (but not the contingency) surface may be even more easily realized than in the method already described.

By condensed correlation tables are to be understood those giving the (weighted) frequencies for a first character x and the first (and where necessary also the second) rough moment about 0 as origin of the associated array of the y character.[3] From such a table[4] r may be quickly obtained[5] and the means of arrays calculated for linearity of regression tests.

In principle, the formation of these reduced tables is very simple. Let $x, y, z, \cdots$, be measures on the individuals of the same or associated classes. Let there be $n, p, q, \cdots$, of these individuals. Then if $n, p, q, \cdots, \Sigma(x'), \Sigma(y'), \Sigma(z'), \cdots, \Sigma(x'^2), \Sigma(y'^2), \Sigma(z'^2), \cdots$ (where Σ indicates a summation within the class and the dashes indicate that the measures are to be regarded as deviations from 0) be again summed for each of the component measures, seriated by grades, the four columns—grade of "first individual," weighted frequency, and the two rough moments about 0 for associated individuals—thus secured for each character either constitute the desired table or one from which it may be easily derived.

The arithmetical routine will be determined largely by the nature of the records. Roughly, two cases are possible: $n, p, q, \cdots$, are small, m is small or large; $n, p, q, \cdots$, are large, m is small,[6] m being the number of classes or groups of classes.

Suppose $n, p, q, \cdots$, small, say 4–20. The best method

[3] In direct intra-class correlations x and y are measures of the same kind; in cross intra-class correlations they are different; in inter-class relationships they may be the same or different.

[4] For example, Table X of *Biometrika*, Vol. 8, p. 61, 1911, or Table II derived from Table I of the AMER. NAT., Vol. 44, p. 695, 1910.

[5] See "The Arithmetic of the Product Moment of Calculating the Coefficient of Correlation," AMER. NAT., Vol. 44, pp. 693–699, 1910.

[6] Cases where both the numbers within the class and the number of classes are large are very rare because of the great labor required in making the observations.

is to write the values of the first character under consideration—designated for convenience as the subject—down the side of a separate sheet for each class. Opposite each entry is then written n, $\Sigma(x')$ and $\Sigma(x'^2)$, p, $\Sigma(y')$ and $\Sigma(y'^2)$, q, $\Sigma(z')$ and $\Sigma(z'^2)$ and so on, according to the relationships desired. Thus, the measure used as the subject and the number and summed first and second powers of deviation of the individuals of the relative array may be for the same or different characters or classes, depending on whether direct or cross, intra-class or inter-class correlation is to be computed. In any case, the number and moments are only once determined for each class—their repeated entry on the sheet is merely rapid clerical work.

This done, the sheets are clipped into strips by subject entries, the strips seriated according to the subject, and the class numbers and moments summed for each grade on the machine.

For inter-class correlations, the resulting table is correct, embracing as it does, say, $S(pq)$ entries. For intra-class relationships, say for x, the entries are too high by $S(n)$, $S(x')$ and $S(x'^2)$ since it comprises $S(n^2)$ entries when only $Sn(n—1)$ are desired. Hence, the actual frequency for each subject grade must be subtracted from the weighted frequency, and the products of the actual frequency by the grade and by the square of the grade must be deducted from the first and second summed moment column, respectively.

When the number of individuals per class, n, p, q, is large (*e. g.*, 25 or over) another procedure is desirable. The classes of the subject character are seriated (in transverse rows) in a table of vertical columns captioned by the grades. Opposite each row is entered n, $\Sigma(x')$ and $\Sigma(x'^2)$, p, $\Sigma(y')$ and $\Sigma(y'^2)$, q, $\Sigma(z')$ and $\Sigma(z'^2)$, $\cdots$, for all characters to be correlated. The associated (weighted) values for each subject grade are quickly gathered by multiplying up and summing simultaneously the fre-

quencies in each column of the subject seriations by the opposed entries in the relative (number and summation) columns. Again, the result is the desired table or one from which it may be derived.

Illustrations will make the methods most clear. Table I shows the frequencies for the different grades of radial asymmetry[7] of quinquilocular fruits gathered from 34 individuals of *Hibiscus Syriacus* in the Missouri Botanical Garden in the fall of 1907. Table II gives the seriations for the locular composition[8] of the same fruits. The last two columns of Table I and the next to the last two of Table II give the first two summations for each individual.[9]

[7] The radial asymmetry is the standard deviation of the number of ovules per locule about the mean number of ovules per fruit. See *Biometrika*, Vol. 7, pp. 476–479, 1910, for full discussion.

At the head of this table the coefficients of asymmetry are for condensation given to only two places. In all the calculations, however, they have been used to six places. Their values and their true squares as used in the calculations are:

Asymmetry a	a^2
.000000	.00
.400000	.16
.489897	.24
.632455	.40
.748331	.56
.800000	.64
.894427	.80
.979795	.96
1.019803	1.04
1.095445	1.20
1.166190	1.36
1.200000	1.44
1.264911	1.60
1.356466	1.84
1.600000	2.56

[8] Expressed here simply as the number of locules per fruit with an "odd" number of ovules. *Cf. Biometrika*, Vol. 7, pp. 483–487, 1910.

[9] The last two columns of Table II give the summations of Table I for convenience in determining the cross intra-class tables. When the cross intra-class tables are to be formed with asymmetry as the subject the $\Sigma(c')$ and $\Sigma(c'^2)$ column may be added to Table I. Here it is omitted for convenience in publication.

TABLE I

SERIATIONS AND SUMMATIONS OF RADIAL ASYMMETRY BY INDIVIDUALS

Tree	Radial Asymmetry—Standard Deviations of Individual Fruits															N	$\Sigma(a')$	$\Sigma(a'^2)$
	.00	.40	.48	.63	.74	.80	.89	.97	1.01	1.09	1.16	1.20	1.26	1.35	1.60			
1	22	25	20	5	14	9	2	—	1	1	—	—	—	—	—	99	44.540951	28.24
2	37	29	19	5	5	2	—	1	1	—	—	—	—	—	—	99	31.411571	17.28
3	46	34	13	2	1	2	—	1	—	—	—	—	—	—	—	99	24.561697	12.16
4	66	29	4	1	—	2	—	—	—	—	—	—	—	—	—	102	15.792043	7.28
5	11	25	33	8	11	4	3	—	4	—	1	—	—	—	—	100	50.586565	31.76
6	14	22	38	13	8	5	2	—	2	—	1	1	—	—	—	106	51.819299	32.00
7	46	30	16	3	3	2	—	—	—	—	—	—	—	—	—	100	25.580710	12.80
8	13	33	29	6	11	3	2	1	1	—	—	—	—	—	—	99	45.621836	26.32
9	13	27	32	4	12	10	1	2	—	—	—	—	1	—	—	102	50.105424	31.04
10	26	40	17	6	4	6	1	1	—	—	1	—	—	—	1	103	40.556715	24.64
11	16	30	25	11	10	4	4	—	—	—	1	—	—	—	—	101	46.631638	27.92
12	8	21	34	14	8	12	1	—	—	—	1	—	—	—	—	99	51.558133	31.44
13	34	19	24	6	3	9	1	1	—	—	—	—	—	—	—	97	34.471473	20.40
14	59	33	4	1	—	—	—	—	—	—	—	—	—	—	—	97	15.792043	6.64
15	13	21	30	10	14	1	2	3	1	1	—	—	—	2	—	98	50.254513	33.44
16	42	28	18	6	1	3	—	1	—	—	—	—	—	—	—	99	27.941002	14.64
17	33	26	22	7	8	4	—	—	—	—	—	—	—	—	—	100	34.791567	19.28
18	50	24	18	2	2	—	—	2	1	—	—	—	—	—	—	99	24.159111	13.04
19	63	18	11	2	2	3	—	—	—	—	—	—	—	—	—	99	17.750439	9.36
20	72	20	6	—	—	1	—	1	—	—	—	—	—	—	—	100	12.719177	6.24
21	41	29	16	4	3	4	—	—	2	—	1	—	—	—	—	100	30.618961	17.76
22	42	21	25	4	5	2	—	1	—	—	—	—	—	—	—	100	29.498695	16.00
23	34	31	19	5	4	4	1	2	—	—	—	—	—	—	—	100	33.917659	19.04
24	31	16	28	1	10	6	3	3	1	—	—	—	—	—	—	99	39.675350	25.44
25	15	33	32	4	6	10	—	1	—	—	—	—	—	—	—	101	44.876305	25.28
26	28	26	21	8	7	5	2	—	1	—	—	—	—	—	—	98	37.794451	22.16
27	56	30	8	3	1	2	—	—	—	—	—	—	—	—	—	100	20.164872	9.76
28	38	34	20	2	3	2	1	—	—	—	—	—	—	—	—	100	29.402270	14.80
29	4	25	35	5	11	11	2	2	—	—	—	1	—	—	—	96	52.288755	32.56
30	40	25	14	5	5	5	3	1	—	—	—	—	—	—	—	98	31.425564	18.72
31	11	27	34	7	9	8	—	2	—	—	1	1	—	—	—	100	49.344442	30.16
32	28	31	12	13	9	2	2	3	1	—	1	—	—	—	—	102	41.749890	26.24
33	28	21	20	4	6	11	4	3	—	—	1	1	—	—	—	99	42.901029	29.04
34	7	34	29	7	13	8	1	1	1	—	—	1	—	—	—	102	52.456526	31.84

TABLE II

SERIATIONS AND SUMMATIONS FOR LOCULAR COMPOSITION BY INDIVIDUALS

Tree	Locular Composition—Number of "Odd" Locules per Fruit						N	$\Sigma(c')$	$\Sigma(c'^2)$	$\Sigma(a')$	$\Sigma(a'^2)$
	0	1	2	3	4	5					
1	25	23	19	22	9	1	99	168	466	44.540951	28.24
2	36	25	18	12	6	2	99	131	351	31.411571	17.28
3	46	36	11	5	1	–	99	77	141	24.561697	12.16
4	67	30	3	2	—	–	102	42	60	15.792043	7.28
5	10	19	24	33	12	2	100	224	654	50.586565	31.76
6	13	18	38	24	11	2	106	220	612	51.819299	32.00
7	44	31	9	13	1	2	100	102	250	25.580710	12.80
8	10	21	25	22	17	4	99	225	691	45.621836	26.32
9	15	27	31	17	9	3	102	191	523	50.105424	31.04
10	31	37	18	10	7	–	103	131	311	40.556715	24.64
11	13	30	25	22	7	4	101	194	540	46.631638	27.92
12	8	27	28	29	6	1	99	199	521	51.558133	31.44
13	35	24	27	6	3	2	97	118	284	34.471473	20.40
14	59	33	4	1	—	–	97	44	58	15.792043	6.64
15	9	19	34	24	8	4	98	211	599	50.254513	33.44
16	42	31	14	11	1	–	99	96	202	27.941002	14.64
17	31	22	23	14	7	3	100	153	427	34.791567	19.28
18	50	26	18	5	—	–	99	77	143	24.159111	13.04
19	66	18	8	7	—	–	99	55	113	17.750439	9.36
20	72	21	5	1	1	–	100	38	66	12.719177	6.24
21	42	27	20	6	4	1	100	106	250	30.618961	17.76
22	41	18	19	15	4	3	100	132	368	29.498695	16.00
23	35	33	14	14	3	1	100	120	288	33.917659	19.04
24	32	19	23	17	6	2	99	150	410	39.675350	25.44
25	17	36	28	14	5	1	101	159	379	44.876305	25.28
26	26	22	23	14	10	3	98	165	475	37.794451	22.16
27	57	31	10	2	—	–	100	57	89	20.164872	9.76
28	38	30	16	9	7	–	100	117	287	29.402270	14.80
29	8	27	31	20	10	–	96	189	491	52.288755	32.56
30	44	27	15	9	3	–	98	96	216	31.425564	18.72
31	11	14	37	14	19	5	100	231	717	49.344442	30.16
32	28	33	24	12	4	1	102	138	326	41.749890	26.24
33	30	26	17	14	5	7	99	157	475	42.901029	29.04
34	7	25	29	21	19	1	102	227	659	52.456526	31.84

TABLE III

LOCULAR COMPOSITION

		0	1	2	3	4	5	Totals
Radial Asymmetry	.000000	1,038	—	—	—	—	49	1,087
	.400000	—	730	—	—	187	—	917
	.489897	—	—	420	306	—	—	726
	.632455	—	—	73	111	—	—	184
	.748331	—	—	179	30	—	—	209
	.800000	45	101	—	—	12	4	162
	.894427	—	37	—	—	1	—	38
	.979795	14	12	—	—	5	2	33
	1.019803	—	—	6	11	—	—	17
	1.095445	—	—	1	1	—	—	2
	1.166190	—	—	8	1	—	—	9
	1.200000	—	5	—	—	—	—	5
	1.264911	—	1	—	—	—	—	1
	1.356466	—	—	1	1	—	—	2
	1.600000	1	—	—	—	—	—	1
	Totals,	1,098	886	688	461	205	55	3,393

TABLE IV

Asymmetry and Asymmetry

Asymmetry	Gross Values			Values to be Deducted			Working Table		
	n	Total a'	Total a'^2	n	Total a'	Total a'^2	n	Total a'	Total a'^2
.000000	108,324	32,152.8593	18,159.68	1,087	000.0000	000.00	107,237	32,152.8593	18,159.68
.400000	91,608	33,189.7416	19,387.04	917	366.8000	146.72	90,691	32,822.9416	19,240.32
.489897	72,526	29,615.2738	17,726.56	726	355.6652	174.24	71,800	29,259.6085	17,552.32
.632455	18,427	7,668.6159	4,616.56	184	116.3717	73.60	18,243	7,552.2441	5,427.28
.748331	20,879	9,099.5847	5,544.32	209	156.4012	117.04	20,670	8,943.1835	5,427.28
.800000	16,162	6,787.1336	4,103.04	162	129.6000	103.68	6,000	6,657.5336	3,999.36
.894427	3,790	1,663.8007	1,030.72	38	33.9882	30.40	3,752	1,629.8125	1,000.32
.979795	3,285	1,318.9137	807.68	33	32.3332	31.68	3,252	1,286.5805	776.00
1.019803	1,707	734.8870	450.56	17	17.3367	17.68	1,690	717.5503	432.88
1.095445	197	94,7955	61.68	2	2.1909	2.40	195	92.6046	59.28
1.166190	910	405.7667	250.96	9	10.4957	12.24	901	395.2710	238.72
1.200000	503	248.8101	155.60	5	6.0000	7.20	498	242.8100	148.40
1.264911	102	50.1054	31.04	1	1.2649	1.60	101	48.8405	29.44
1.356466	196	100.5090	66.88	2	2.7129	3.68	194	97.7961	63.20
1.600000	103	40.5567	24.64	1	1.6000	2.56	102	38.9567	22.08
	338,719	123,171.3535	72,416.96	3,393	1,232.7607	724.72	335,326	121,938.5929	71,692.24

TABLE V

Locular Composition and Asymmetry

Locular Composition	Gross Values			Values to be Deducted			Working Table		
	n	Total a'	Total a'^2	n	Total a'	Total a'^2	n	Total a'	Total a'^2
0 odd	109,418	32,490.3521	18,369.20	1,098	51.3171	44.80	108,320	32,439.0350	18,324.40
1 odd	88,448	31,547.4534	18,410.64	886	424.9163	231.36	87,562	31,122.5371	18,179.28
2 odd	68,767	28,239.0889	16,957.92	688	403.7775	250.40	68,079	27,835.3114	16,707.52
3 odd	46,075	19,480.3436	11,759.60	461	257.3969	150.48	45,614	19,222.9468	11,609.12
4 odd	20,521	9,073.6754	5,490.16	205	90.1934	43.20	20,316	8,983.4820	5,446.96
5 odd	5,490	2,340.4401	1,429.44	55	5.1596	4.48	5,435	2,335.2805	1,424.96
	338,719	123,171.3535	72,416.96	3,393	1,232.7607	724.72	335,326	121,938.5928	71,692.24

From I and II, the machine quickly compiles four working tables—a direct intra-class for asymmetry, a, and another for locular composition, c, and two cross intra-class tables.[10] The columns under "gross values" in

TABLE VI

ASYMMETRY AND LOCULAR COMPOSITION

A	Gross Values			Values to be Deducted			Working Table		
	n	Total c'	Total c'^2	n	Total c'	Total c'^2	n	Total c'	Total c'^2
.00	108,324	117,335	288,699	1,087	245	1,225	107,237	117,090	287,474
.40	91,608	127,391	332,887	917	1,478	3,722	90,691	125,913	329,165
.48	72,526	117,550	318,254	726	1,758	4,434	71,800	115,792	313,820
.63	18,427	30,358	81,952	184	479	1,291	18,243	29,879	80,661
.74	20,879	36,577	100,993	209	448	986	20,670	36,129	100,007
.80	16,162	26,180	70,560	162	169	393	16,000	26,011	70,167
.89	3,790	6,549	18,093	38	41	53	3,752	6,508	18,040
.97	3,285	5,014	13,422	33	42	142	3,252	4,972	13,280
1.01	1,707	3,040	8,460	17	45	123	1,690	2,995	8,337
1.09	197	379	1,065	2	5	13	195	374	1,052
1.16	910	1,600	4,406	9	19	41	901	1,581	4,365
1.20	503	1,024	2,954	5	5	5	498	1,019	2,949
1.26	102	191	523	1	1	1	101	190	522
1.35	196	422	1,198	2	5	13	194	417	1,185
1.60	103	131	311	1	0	0	102	131	311
	338,719	473,741	1,243,777	3,393	4,740	12,442	335,326	469,001	1,231,335

TABLE VII

LOCULAR COMPOSITION AND LOCULAR COMPOSITION

Loc. Comp.	Gross Values			Values to be Deducted			Working Table		
	n	Total c'	Total c'^2	n	Total c'	Total c'^2	n	Total c'	Total c'^2
0	109,418	117,758	288,576	1,098	0,000	0,000	108,320	117,758	288,576
1	88,448	118,815	305,713	886	886	886	87,562	117,929	304,827
2	68,767	111,775	302,475	688	1,376	2,752	68,079	110,399	299,723
3	46,075	78,151	213,853	461	1,383	4,149	45,614	76,768	209,704
4	20,521	37,538	105,540	205	820	3,280	20,316	36,718	102,260
5	5,490	9,704	27,620	55	275	1,375	5,435	9,429	26,245
	338,719	473,741	1,243,777	3,393	4,740	12,442	335,326	469,001	1,231,335

Tables IV–VII give the results. These contain, since $p=q$, a total $S(p^2)=S(q^2)=S(pq)$ entries, whereas in the direct intra-class relationships $S[p(p-1)]=S[q(q-1)]$, and in the cross intra-class $S[p(q-1)=S[q(p-1)]$ are desired.

[10] One for the relationship between radial asymmetry and locular composition, the other for the correlation between locular composition and radial asymmetry. Of course, both give the same end result, and only one need be found unless the linearity of both regressions is to be tested.

From these gross values must be deducted, therefore, the actual frequency for each grade of the subject and the product of the frequency by the first and second power of the grade in the case of direct intra-class correlation, or the frequency of the grade and the sum of the first and second powers of the values of the relative character in the same fruit in the cross intra-class correlation. Data for these are given in the table showing the correlation for asymmetry and locular composition of the same fruit, Table III. The second set of three columns in Tables IV–VII gives the quantities so calculated from Table III to be deducted. The final three columns are in each case the working tables.

The first and second moments for the (weighted) population A and σ are given by the totals of the two final columns. Or those for the subject character may be calculated (and a check for the accuracy of the totals secured) from the grade of the subject and the weighted frequency column.[11]

From our working tables, indicating by S a summation from our final tables, we determine by the methods of AMER. NAT., Vol. 45, pp. 693–699, 1910, these values:

For Asymmetry

$$S(a') = 121{,}938.5928, \quad A_a = .363642,$$
$$S(a'^2) = 71{,}692.2400, \quad \sigma_a = .285593.$$

For Locular Composition

$$S(c') = 469{,}001, \quad A_c = 1.398642,$$
$$S(c'^2) = 1{,}231{,}335, \quad \sigma_c = 1.309906.$$

For Asymmetry and Locular Composition

Table IV, $S(a_1'a_2') = 48{,}818.9505, \quad r = .1637,$
Table VI, $S(a_1'c_2') = 192{,}072.3309,$[12] $r = .1716,$
Table V, $S(c_1'a_2') = 192{,}072.3308,$[12] $r = .1716,$

[11] Of course in practise, the second population moment may be calculated by $S[(n-1)\Sigma(x'^2)]$, $S[(p-1)\Sigma(y'^2]$, $S[(q-1)\Sigma(z'^2)]$, . . . , thus obviating the labor of forming the third columns, which are included here for completeness of illustration merely.

[12] The difference of .0001 is due to the necessity of lopping off the last two places of the six decimals in the asymmetry coefficient in the one case while they can be retained in the other. Of course, it is of no practical significance.

Table VII, $S(c_1'c_2') = 763{,}048.0000$, $r = .1861$.

While primarily illustrations of method, these results, if they are substantiated by further work, seem to me of considerable biological interest. They show not only that individuals of *H. Syriacus* differ in the radial asymmetry and in the locular composition of their fruits, but that when an individual bears fruits above the average asymmetry, it also produces fruits above the average in number of "odd" locules. Apparently, this cross correlation is as high as either of the direct correlations.

Two biological interpretations are possible. (*a*) The production of radially symmetrical ovaries and those with a high number of odd locules depends upon the same morphogenetic tendencies of the primordia,[13] which give rise to the fruit. (*b*) There is in *Hibiscus* an intra-individual selective elimination similar to that demonstrated in *Staphylea*,[14] the intensity of which differs from individual to individual in such a way as to bring about (statistical) correlation for characters originally uncorrelated.

The discussion of these points falls outside the scope of the present note where the data serve merely as a random illustration of a very rapid method of carrying out the routine of a widely applicable statistical process.

COLD SPRING HARBOR,
April 25, 1912

[13] In the individual fruit radial asymmetry and locular composition are necessarily associated (*cf. Biometrika*, Vol. 7, pp. 491–493, 1910). In *Staphylea*, correlations of $r = .22$ to $r = .33$ have been noted. Table III above gives $r = .527$ for asymmetry and locular composition of the same fruit.

Probably in all these relationships regression is not linear, and the correlations must be interpreted with caution.

[14] *Biometrika*, Vol. 7, pp. 452–504, 1910; *Science*, N. S., Vol. 32, pp. 519–528, 1910; *Zeitschr. f. Ind. Abst. u. Vererbungsl.*, Vol. 5, pp. 273–288, 1911; *Pop. Sci. Mo.*, Vol. 78, pp. 534–537, 1911.

SHORTER ARTICLES AND DISCUSSION

PRODUCTION OF PURE HOMOZYGOTIC ORGANISMS FROM HETEROZYGOTES BY SELF-FERTILIZATION

HAS any one worked out formulæ for determining the rate at which organisms become homozygotic through continued self-fertilization? The problem is of interest in various connections, but principally perhaps with relation to the "pure line" work. Johannsen worked, for example, with self-fertilizing beans that are held to be homozygotic in all respects. I have often heard the questions raised: How probable is it that such plants really are homozygotic? Is it indeed possible that they have reached a purely homozygotic condition?

I have not come across a working out of this matter, and finding it necessary to deal with the problem in connection with studies of inheritance in *Paramecium*, it will perhaps be useful if I put on record the results.[1]

The principles which underlie the matter are the following: (1) In self-fertilized organisms, all characteristics that become once homozygotic, remain homozygotic forever after, since there is no method in self-fertilization of introducing a gamete that is diverse in this respect; (2) characteristics heterozygotically represented become homozygotic in a certain proportion of the offspring. The problem becomes essentially this: in what proportion do the heterozygotic characters become homozygotic, and how great a proportion of all the organisms will therefore have become thus homozygotic after a given number of self-fertilizations?

Suppose that we begin with an organism in which all separable characters are heterozygotically represented.

1. Consider first a single pair of such alternative characters, which we may call $\left\{\begin{matrix} A \\ a \end{matrix}\right.$. The gametes produced will be A, a,

[1] At the moment of receiving the proof of this note I receive also the masterly paper of East and Hayes ("Heterozygosis in Evolution and in Plant Breeding," Bulletin 243, Bureau of Plant Industry, June 5, 1912), in which this matter is dealt with and a general formula given. "The probable number of homozygotes and any particular class of heterozygotes in any generation r is found by expanding the binomial $[1 + (2^r - 1)]^n$, where n represents the number of character pairs involved," etc. (p. 21). Possibly the present note may still be useful.

A, and a, and when these combine in all possible ways, they give zygotes $AA + Aa + aA + aa$; that is, two homozygotes and two heterozygotes. Thus, the self-fertilization of such an organism gives ½ the progeny homozygotic (with respect to this characteristic); ½ heterozygotic. If we let x = the proportion of homozygotes, y the proportion of heterozygotes (with respect to one character), then after the first self-fertilization

$$x = ½ \text{ of all.}$$
$$y = ½ \text{ of all.}$$

Now, after the next self-fertilization, of course the homozygotes x remain pure, so that half of all the progeny are still homozygotes on this account. The heterozygotes y of course again break up, in the way already set forth, one half into x, the other half remaining y. Since y included half of all, this will give ½ of ½ (= ¼ of all) as x, ½ of ½ (= ¼ of all) as y.

So the total proportion for the homozygotes x becomes after the second fertilization

$$x = ½ + (½)^2 = ¾,$$

while

$$y = (½)^2 = ¼.$$

This process is repeated after each fertilization, so that if there are n fertilizations in succession, the total number of homozygotes x, becomes

$$x = ½ + (½)^2 + (½)^3 \ldots \text{ up to } (½)^n.$$

This expression reduces to $x = \dfrac{2^n - 1}{2^n}$, where n is the number of fertilizations.

For the heterozygotes, y, on the other hand the formula is simply

$$y = (½)^n.$$

These then are the formulæ in case we deal with but one pair of characters. They express (1) the proportion of all the organisms that will be homozygotic (or heterozygotic as the case may be), after a given number n of fertilizations; (2) also they of course express the relative probability for a given case, as to whether it shall be homozygotic or heterozygotic.

2. When we are to deal with two or more pairs of characters, the problem may be attacked in two ways. One is by the general principles of probabilities; the other is by analyzing the case of two or more characters in the way exemplified above. The two methods give the same results.

The first method is far the simpler. It is merely an application of the principle that when we know the probability for

each of two or more things separately, the probability that all of them shall happen is the product of the separate probabilities for each. Now, we know that the probability x for the homozygotic condition with respect to one character is

$$x = \frac{2^n - 1}{2^n}.$$

For two characters it is then

$$\left(\frac{2^n - 1}{2^n}\right) \times \left(\frac{2^n - 1}{2^n}\right); \quad \text{or} \quad \left(\frac{2^n - 1}{2^n}\right)^2.$$

For three characters it is of course $\left(\frac{2^n - 1}{2^n}\right)^3$, and in general, for any number m of characters, the probability x for pure homozygotes (or the proportional number of pure homozygotes) is

$$x = \left(\frac{(2^n - 1)^m}{2^n} \cdot\right)$$

By similar reasoning, the proportion of all the organisms that will be heterozygotic with respect to all the m characters is

$$y = (\tfrac{1}{2})^{nm}.$$

With two or more characters, there will be of course a considerable number of the organisms that are homozygotic with respect to some characters, heterozygotic with respect to others. If we call the proportion of these z, then

$$z = 1 - (x + y).$$

And if we let v be the total proportion that contains any heterozygotic characters (so that $v = y + z$), then

$$v = 1 - \left(\frac{2^n - 1}{2^n}\right)^m = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}.$$

These formulæ may readily be deduced algebraically, or verified, by a detailed analysis of a case of two or more characters. It may be worth while to indicate the method followed, by taking up the simpler case of two pairs of characters. Call these $\left\{\begin{matrix} A \\ a \end{matrix}\right.$ and $\left\{\begin{matrix} B \\ b \end{matrix}\right.$. The gametes formed are *AB*, *Ab*, *aB*, and *ab*. When these combine in all possible ways (as indicated in the diagrams given in Bateson's Mendelism), these give the following results:

$$1ABAB + 1AbAb + 1aBaB + 1abab + 2ABab +$$
$$2AbaB + 2ABAb + 2ABaB + 2Abab + 2aBab = 16.$$

It will be observed that of the entire 16, the first four are pure homozygotes, the second four are pure heterozygotes (heterozy-

gotic with respect to both characters); while the last 8 are mixed (homozygotic with respect to one character, heterozygotic with respect to the other). Letting x = pure homozygotes, y = pure heterozygotes, z = mixed, we find thus that

$$x = 1/4,\ y = 1/4,\ z = 1/2, \text{ of all.}$$

Now, by an analysis of the sort already given, it will be found that at the next self-fertilization, x remains x; y breaks up, $1/4$ of these becoming x, $1/2$ becoming z, and $1/4$ remaining y; z breaks up, $1/2$ of these becoming x, $1/2$ remaining z.

Now, when we recall that before the second fertilization x was $1/4$; y, $1/4$, and z, $1/2$ of all, we see from the above that after the second fertilization

$$x = 1/4 + (1/2 \times 1/2) + (1/4 \times 1/4) = 9/16 = \left(\frac{2^n - 1}{2^n}\right)^2,$$

$$y = (1/4 \times 1/4) = 1/16 = (1/2)^{2n},$$

$$z = (1/2 \times 1/2) + (1/2 \times 1/4) = 3/8 = (1/2)^n + (1/2)^{n+1}.$$

These are the same formulæ for x and y that were obtained by the other method (since here n and m are each 2). This method however gives in addition a direct formula for z.

It is easy to verify the formulæ for three pairs of characters, though of course the conditions become here somewhat more complex.

We may now summarize our formulæ, and show the results they give in certain examples.

Let x = the proportional number of organisms that are pure homozygotes (with respect to all the characters considered),

y = the proportion that are heterozygotic with respect to all the characters considered,

z = the proportion that are mixed,

v = the proportion that have any heterozygotic characters.

Then, if n = the number of successive self fertilizations and m = the number of pairs of characters,

$$x = \left(\frac{2^n - 1}{2^n}\right)^m, \tag{1}$$

$$y = (1/2)^{mn}, \tag{2}$$

$$z = 1 - (x + y), \tag{3}$$

$$v = 1 - x = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}. \tag{4}$$

Examples.—(1) Suppose that there have been eight self-fertilizations, and that we are dealing with 10 pairs of characters. What proportion x of the organisms will be homozygotic with

respect to all the 10 characters? What proportion will be homozygotic with respect to any given one character? To any two or three?

Taking first the case for the entire 10 characters, by formula (1)

$$x = \left(\frac{2^8 - 1}{2^8}\right)^{10} = \left(\frac{255}{256}\right)^{10} = \text{log. } 9.9830020 = .961617.$$

Thus, out of 100 individuals, somewhat above 96 would be pure homozygotes; or by formula (4), but one in 26 would be heterozygotic in any respect ($v = .038383$).

With respect to any one character formula (1) gives

$$x = \left(\frac{2^8 - 1}{2^8}\right)^{1} = \frac{255}{256} = .99609375,$$

so that all but 4 in 1,000 would be homozygotes with respect to that character.

In the same way we find that with respect to any two characters the proportion of homozygotes would be .9922; with respect to three, .9883; with respect to four, .9845, etc.

(2) Suppose that there are 20 pairs of characters, and that there have been 20 self-fertilizations. Then

$$x = \left(\frac{2^{20} - 1}{2^{20}}\right)^{20} = \left(\frac{1{,}048{,}575}{1{,}048{,}576}\right)^{20} = \text{log. } 9.9999957 = .999998.$$

That is, of a million individuals, all but two would be pure homozygotes.

It thus appears that if the number of separably heritable characters is not very great (say not above 100), while the organism has been self-fertilized for many generations, it is to be expected that practically all of the organisms will be homozygotic with respect to all their characters, they will be "pure homozygotes."

H. S. JENNINGS

YELLOW AND AGOUTI FACTORS IN MICE NOT "ASSOCIATED"

IN a recent number of the AMERICAN NATURALIST Mr. Sturtevant[1] suggests that these two color factors may bear to each other the relation which Bateson has called "repulsion" or "spurious allelomorphism" and which Morgan now includes with "coupling" in a more general category, "association." The supposed

[1] Sturtevant, A. H., "Is there Association Between the Yellow and Agouti Factors in Mice?" AM. NAT. Vol. XLVI, No. 546, p. 368, 1912.

relation is such that the characters involved fail to pass into the same gamete even though they may be present together in the parent zygote. That yellow and agouti in mice are not in general so related is shown conclusively by experiments which will be more fully described elsewhere, but which may be briefly summarized in the following table:

Mating	Parents	Offspring		
	Both Yellow	Yellow	Agouti	Black or Brown
185	894×895	1	1	5
10	502.2A×502.5A	10	2	1
397	3,908×875	4	2	2
273	2,049×875	5	1	1
159	786×784	5	3	1
446	Unmarked×4,054	8	6	2
500	Unmarked×4,152	2	3	1
545	Unmarked×4,152	4	2	1
467	4,524×4,523	9	1	1
519	Unmarked×4,631	6	2	1
543	———×4,905	2	1	3
397	3,908× 875	4	2	2
240	1,828×1,829	10	1	6
113	562× 563	6	3	2
173	1,074× 563	2	1	2
	Total	78	31	31

In these experiments yellow animals bred *inter se* have produced non-yellow young half of which are agouti and half of which are non-agouti. It seems therefore to be wholly a matter of chance whether a yellow animal heterozygous in agouti transmits that character *with* yellow or apart from it. Sturtevant's contrary conclusion is due in part to his reliance on the insufficient numbers observed by Morgan and in part to his overlooking certain of the results reported by Miss Durham. For, in addition to the category of matings of yellow mice cited by Sturtevant, she reports matings of sable (yellow) mice *inter se* which produced 17 sable (yellow), 8 yellow, 5 agouti, 4 black, and 2 brown young, a result in harmony with that which I have described.

In the matings reported by Miss Durham in which yellow parents produced only yellow young and agouti young, it seems probable that one or both of the yellow parents was homozygous in agouti. The same was probably true in the similar experiments of Morgan. This would explain why all the non-yellow young were agouti marked.

As further evidence that yellow and agouti are wholly independent characters may be cited experiments of my own in which yellow animals evidently heterozygous in agouti were

mated with brown animals which invariably lack agouti. There were produced 15 young, of which 7 were yellow, 5 agouti and 3 black or brown. Evidently the yellow parent transmitted non-yellow (black or brown) in 5 cases associated with agouti, and in 3 cases not so associated. On Sturtevant's hypothesis all non-yellow young should have been agouti.

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June 17, 1912

PHYSICAL ANALOGIES OF BIOLOGICAL PROCESSES

Two schools or methods of thinking of heredity and other general problems are recognized among biologists. Some hold that all biological phenomena are to be explained in terms of physical and chemical properties of unorganized matter. Others are inclined to believe that the activities of living matter represent agencies or relations not shown in the inorganic world. The first view has been called materialism, the second vitalism.

These distinctions are not as important as sometimes supposed, because of our inadequate knowledge of the properties of matter, whether organic or inorganic. The materialistic view may be said to have a practical advantage in encouraging the investigation of the physical and chemical phenomena of the organic world, but vitalism may claim at least an equal advantage in permitting the recognition of facts that lie on the other side of the biological field, where the analogies of physics and chemistry find little or no application. Thus the specific constitution or speciety of living matter, the fact that organisms maintain their existence and make evolutionary progress only in groups of individuals united into specific networks of descent, involves the recognition of a condition or property quite foreign to the usual conceptions of the physicist or the chemist. Yet this universal condition of speciety must be considered as a general basis or background for any strictly biological study of the organic world. We may count, weigh, measure or analyze the bodies and activities of organisms from as many other standpoints as we please, but it is idle to draw general biological conclusions from any merely mathematical or physical data. The true biological significance of statistical and physical facts has to be determined by biological analysis.

As long as physical and mathematical analogies add something to our comprehension of biological facts they are entirely

desirable and legitimate. Even an incomplete and inadequate analogy may be very useful for descriptive purposes. But when the elaboration of an analogy interferes with perception of the fact it is supposed to elucidate the limitations of the method become apparent. This danger may be illustrated by a recent attempt to define biological evolution in physical terms.

In the minds of most of us the term "evolution" is associated probably more closely with the biological than with the physical sciences. Yet the concept is essentially physical in character, and is definable in exact terms probably only in the language of physics. For in its last analysis we may define evolution as *the history of a material system undergoing irreversible transformation.* To the physicist, therefore, the study of evolution is essentially the study of irreversible changes, and the law of evolution is the law of increasing entropy, or, more generally, of the increasing probability of the successive states of any real material system.[1]

Whether such definitions have any practical advantage as aids to further investigation may be questioned. Exact terms are of little use in biology unless they are also concrete, that is, unless they convey an idea of something that can be seen, or at least imagined. Physicists are much more tolerant of mathematical and metaphysical abstractions. The habit of using abstract conceptions often leads to the announcement of wonderful discoveries that resolve themselves, on closer inspection, into purely metaphysical manipulations of terms. Thus it is considered one of the notable services of a "supreme biologist" that he should have identified chemical reactions with organic tropisms, tropisms with instincts, instincts with morals, and then predicted a chemical analysis of morality.[2]

Such inferences only show that the vocabulary has been thrown into solution, not that any concrete insight has been gained. Physical terms can be set into formulæ as mystical as a wizard's incantations. Sleight of hand is discredited, but verbal miracles are still performed with "scientific principles." When so-called physical science runs to seed in antinomies it becomes plain that we are back again in the vicious circles of metaphysical deduction.

To describe biological evolution as a process of irreversible transformation seems especially inappropriate because it is of

[1] Lokta, Alfred J., "Evolution in Discontinuous Systems," *Journ. Wash. Acad. Sciences,* Vol. II, No. 1, 1912, pp. 2–4.

[2] "The Chemistry of Morals," *Current Literature,* 52: 180, February, 1912.

the very nature of biological changes to be reversible, or recurrent in each generation. Only by limiting the idea of evolution to changes in the underlying mechanism of transmission could the specification of irreversibility be made to apply.

Nor is there justification for considering biological evolution under the caption of discontinuous systems. Variations, in the sense of changes of expression of characters, are often discontinuous, but this does not mean that evolution is discontinuous. Some biologists have supposed that new characters constitute new species, but in reality we have to think of the old species as developing the new characters instead of the characters originating the species. As long as species are considered only in a statistical or biometrical sense, the existence of different species will appear to rest on evidence of mathematical discontinuity. But for any truly biological purposes such discontinuity must be considered as a result of evolution, rather than as a condition or cause of evolution. All characters, in the evolutionary sense of the word, are first presented as differences among the members of species. Such differences are always variable, or alternative in expression, which is another way of saying that they are reversible; that is, they appear and disappear, or are expressed in various degrees, in the different individuals belonging to the same specific group.

The phenomena of mutation represent discontinuity among members of the same species, rather than differences between species. Natural species seldom have the same kinds of differences as mutative variations. The theory that species originate by mutative changes of characters is well calculated to deceive physicists and biometricians who are not familiar with the facts of diversity in natural species. Ortmann diagnosed the difficulty with the mutation theory by saying that DeVries does not know what a species is. Familiarity with species is seldom considered as a necessary qualification for the study of evolution and heredity. Indeed, most of our physiological and mathematical biologists have dismissed species as something too indefinite for their purposes. They prefer to begin with a definition that can be stated in exact terms and turned into figures or formulæ. The casual choice of words like irreversible or discontinuous becomes fraught with a vast importance, seldom mitigated by any appreciation of the fact that most of the language of biology is merely descriptive and comparative, and hence to be understood only in relative senses.

If we cut through a tree top it will appear that the branches are discontinuous, but if we follow individual branches this

effect of discontinuity is lost. For some purposes the process of growth might be described as continuous or gradual, and for other purposes as discontinuous, for there are daily interruptions or variations in the rate of growth. Darwin compared the evolution of species to the growth of branches on a tree. Theories that would supplant Darwin's conception of continuity in the evolution of species are not based on equal familiarity with the facts. Constructive evolutionary progress comes by gradual changes in the characters of species, not by saltatory transformations of one species into another. That albinism and other defects appear as mutations and show Mendelian inheritance does not destroy or even conflict with the evidences of continuity in the evolution of species.

The many different applications that can be made of such terms as continuity or discontinuity show how little is gained by the choice of any particular statement of biological facts as a basis for deduction or mathematical elaboration. That new facts can be learned by syllogizing is no longer believed. Is more to be gained by turning syllogisms into mathematical formulæ? Even when physical analogies can be more definitely drawn the biological relations of the facts seldom permit any complete application of mathematical methods of thought.

Taking evolutionary deviations into account, the recurrent life cycles of organisms could be considered as spirals and this might appear to bring them within the range of mathematical treatment. Yet no regularity of form could be ascribed to such spirals, for evolutionary intercalations of new characters are not merely additions at the ends of definite series, but are likely to intervene in any part of the life cycle. Moreover, such intercalations are made without throwing the remainder of the cycle out of adjustment.

From the historical standpoint evolution may be presented as a series of transformations, but from the standpoint of heredity the results must be treated as permanent and coexistent, not merely as successive reactions. Each member or part of the cycle must be supposed to carry the determinants or potentialities, the powers of reproducing every other part. And we know further that these potentialities continue to be carried in latent or recapitulated form, even after they have ceased to come into normal expression. In other words, the biological system retains latent possibilities of reversion, the maps, as it were, of courses of development long since abandoned. Even though the characters be considered as irreversible in the sense of having permanent transmission they are subject nevertheless

to endless vicissitudes of internal and external relations that influence the expression of characters.

Thus the life-cycle spiral is not a single line, but is resolved into a vast multiplicity of lines, tracing back to all the different ancestors. The expression relations of the characters can be analyzed, in a measure, by breeding experiments and by comparing behavior under different conditions, but the nature of the system is such that its most permanent and stable adjustments are those that are farthest removed from the influences of the environment. Hence the futility of mathematical treatments that attempt to combine environmental vicissitudes with the entirely inconsistent facts of biological evolution. Instead of evolution representing a law of increasing probability of successive states, the contrary would be more nearly true. The more specialized the organization the less the probability of passing to another state. Thousands of species are extinguished to one that develops a higher type of organization. Instead of evolution representing a summarized result of environmental influences, it is rather to be considered as a history of ways of avoiding such influences. There are no facts to show that evolutionary progress is caused by environmental agencies or by internal mechanisms. The causes of evolution lie in the structure of the species.

The crowning complexity of the biological system is that the life-cycle spirals do not remain separate and distinct from each other, but are thoroughly interwoven to form a continuous network of descent for each species or group of interbreeding individuals. It may be that a mathematical formula could be made for a spiral wire mattress or a Turkish rug, but this would afford only a faint analogy for the complications that attend the evolution of a species. To describe a species as a network of descent may be only a figure of speech, lacking altogether in mathematical exactness, but it is a way of pointing out a concrete biological fact. When the facts are essentially complex any statement that conceals or disregards the complexity is to that extent specious and misleading.

Many of the results of evolution can be described in simple terms of quantity or sequence, but to consider such statements as definitions, or to suppose that they confer any special license for mathematical elaboration, is to disregard the true nature of the facts and problems of biology. For purposes of physics or chemistry individual plants or animals may be considered as machines, but for purposes of evolution the whole species represents the machine in which the patterns of new characters are

woven. If mathematical elaboration is to serve any useful purpose in showing how evolutionary progress is made the nature of the machine, the specific organization or speciety of the organic world, must be recognized.

O. F. COOK

WASHINGTON, D. C.,
March 15, 1912

ON FAIRNESS AND ACCURACY IN SCIENTIFIC REVIEWING

TO THE EDITOR OF THE AMERICAN NATURALIST: Any one who takes a turn at the critical hoe with the object of ridding the biological field of some of the noxious products of fertile imaginations untrammeled by quantitative facts must expect just the sort of attack which appears in your recent issue (AMER. NAT., March, 1912, p. 165).

1. Dr. Spillman has not felt the purpose, methods or results of my paper worth statement. Instead he illustrates by it the "noticeable degree of correlation between positiveness of statement and inaccuracy of statement." And for the reason: "in Dr. Harris's paper he represents me as having cited the fact [*sic*] that these genotype norms [*sic*] form a frequency curve [*sic*] as proof of the genotype hypothesis [*sic*]."

One excuses the minor inaccuracies and would be glad to pass over the whole assertion with the simple comment that it seems unjust, but to protect himself against further accusations of "inaccuracy of statement" he must add, it is not true.

What I did do was to cite Dr. Spillman among three others in substantiation of the opening sentence, "Several times recently we have been told that the means of a character in a series of pure lines form a 'Quetelet's curve.'" I based this on his statement concerning pure lines, "They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under 'Quetelet's Law'" (AMER. NAT., Vol. 44, p. 760). Surely no injustice has been done so far. Later in the paper I did make a statement (which still holds true) remotely similar to the one quoted above, and said specifically "A case in point is a paper by Roemer." There was no reference whatever to Dr. Spillman—expressed, suggested, insinuated, intimated, implied, . . . or intended.

2. Although it is clearly without any justification, the foregoing criticism would, it seems to me, have gained in strength by specificity and moderation of statement. But Dr. Spillman con-

tinues: "I have not been able to find time to look up other similar citations to see whether the same inaccuracy applies to them." There are *four* "similar citations": one to a paper Dr. Spillman has already read, or at least reviewed for the AMERICAN NATURALIST (Vol. 44, p. 761), one to a few lines in the German *Zeitschrift* for genetics, one to thirteen lines in the AMERICAN NATURALIST (Vol. 45, p. 423) reviewing the fourth, which has again been considered in these pages (AMER. NAT., Vol. 45, pp. 686–700).

3. Dr. Spillman reiterates: "It is now fairly well established that the norms of a group of related genotypes can, in some cases at least, be arranged in a frequency curve." Thus, he tells us, genotypic differences fall under de Vries's category of fluctuating variation, while in discontinuous variation "the norms can not be thus arranged."

Personally, I have not the slightest prejudice against these conclusions, but I can not accept them without proof. Dr. Spillman cites none. *So far as I have been able to ascertain* there is not a single series of trustworthy quantitative data in support of these pregnant generalizations.

4. I acknowledge my fault in omitting *homozygous*. This *was* a serious blunder on my part! By including it, one can always reason in a circle and to prove his preconceptions assume that the original ancestors of a line were or were not homozygous, according to the outcome of his experiments. This is the loophole through which the supple genotypist can always crawl when the evidence on the other side gets a little too strong. Again, in the genotypic ritual, "I wish to publicly repent."

5. But is not the reviewer a little over-zealous when he continues, "the definition is further inaccurate in including clonal varieties under the definition of genotype"? In doing this I merely followed the example of the best specialists. My paper was correct in terminology, as I believe it still is in facts, when it went to press. Several months after the paper Dr. Spillman is criticizing appeared, changes in terminology were forced by "the dictator of the whilom orthodox" genotypic "school"!

J. ARTHUR HARRIS

NOTES AND LITERATURE

DISTRIBUTION AND ORIGIN OF LIFE IN AMERICA[1]

The aim and scope of Scharff's very welcome book is well stated in his own closing words (p. 435): "I have endeavored in this work to show how the gradual evolution of our continents and the former changes of land and water can be demonstrated by a study of the geographical distribution of living animals and plants. Whenever possible I have taken advantage of our paleontological and geological knowledge in furtherance of this object, and I venture to think that I have succeeded in unraveling some intricate problems of the paleogeography of America. Indirectly I have thus been able to indicate the manner in which North and South America became populated and the extent to which these continents took part in supplying animals and plants to other regions of the world." Scharff has certainly done all this and much more besides. Never before has a book upon zoogeography appeared culling and collating the thoughts and observations of such a host of investigators. The fact that his evidence comes not only from practically every group of the animal kingdom, but very often from plants as well, make the deductions far more convincing, radical as they often are, than they would ever be otherwise. Extensive as is the bibliography, there are still a few unfortunate omissions, and some typographical errors mar an otherwise excellent piece of press-work. In the second edition, which can not but appear, the use of titles would wisely be omitted. The words "Professor," "Dr." and "Mr." are used in a rather promiscuous manner. They are not always judiciously bestowed.

The fifteen chapters take up the study of the fauna of the hemisphere, beginning at the north with Greenland and proceeding southward.

In Chapter I the relation of the fauna of Greenland to both Europe and America is convincingly dealt with and Scharff's first excellent map shows the Pliocene bridge which extended from Great Britain through the Orkneys and Iceland to Greenland and on across to Arctic America. In this chapter the ques-

[1] "Distribution and Origin of Life in America." By R. F. Scharff. New York, The Macmillan Co., 1912. Pp. viii + 497, 21 maps.

tion "Did animals survive the ice age?" is first mooted and Scharff prepares us for what is perhaps the most welcome and far-reaching opinion which he, we think successfully, endeavors to prove. His belief is that we have been accustomed to entirely misjudge the extent and importance of the glacial epoch and to exaggerate excessively the part which it has played in influencing the distribution of our present flora and fauna. In this the reviewer heartily agrees and recalls that in Percival Lowell's "Evolution of Worlds" the question is attacked from an entirely different standpoint and a similar conclusion reached. Scharff concludes that "The prevalent geological opinions as to the nature of the Ice Age thus dominate all biological thought in reference to problems of distribution." If we emancipate ourselves from these preconceived notions in our speculations on the origin (for example) of the existing fresh-water mussel fauna, we must arrive at different conclusions.

In Chapter II, then, we have discussed the general features of the fauna of northeastern North America with special reference to this theory of a comparatively insignificant Ice Age.

The third chapter deals with the animals of the Canadian northwest. Ptarmigans, lemmings and gophers, the bison, wapiti deer, our tree porcupine, etc., are discussed and their origin pointed out. There is, however, no reason for concluding, as Scharff does, that the American magpie is more similar to the European form than the Asiatic. All these palæarctic races of magpies are so closely related and the differences between them are so slight as not to permit of any such conclusions as Scharff draws from them. The other chapters on North America deal with the fauna of the Rocky Mountains, the animals of the eastern states, the fauna of the Continental basin and of the southeastern states and Bermuda. In this chapter we meet again with an opinion which, while it can not but gain ground as time goes on, now seems radical in the extreme. Bermuda has always been considered a most typical "oceanic island," yet here we have the view advanced, and well defended, that Bermuda is the remnant of an ancient belt of land which joined it to a southern land mass extending across the Atlantic Ocean. This would account for the presence of both European and American elements in the indigenous fauna, one which, as Scharff shows, is composed wholly of types bearing "the impress of vast antiquity."

In the following chapter (No. IX) we have more detailed dis-

cussion of this bridge between the old and new worlds. In spite of the fact that there are still a considerable number of naturalists who adhere to the old dicta regarding the permanence of land forms and ocean basins, there can be but little doubt that the open-minded student will be convinced by what Scharff has to say regarding the absolute necessity of postulating extensive changes in the forms of the continents to account for the present distribution of animals and plants.

Next follows a discussion of Central America and the West Indies (Chapters X and XI). The fauna of both these regions is carefully analyzed and the very many seeming anomalies of discontinuous distribution are explained, often for the first time, by postulating a series of geographical changes far too elaborate to attempt to summarize in a short review. Suffice it only to say that the treatment of the Lesser Antilles is disappointing and the important part which they have played in joining Antillea (sometimes also spelled Antillia), if perhaps only for a very short time, with that region which is now northeastern South America, is overlooked or receives but scant consideration. The existence of Onycophoran types on many of the Lesser Antilles should have suggested further investigation.

The twelfth chapter deals wholly with the origin and relationship of the fauna of the Galapagos Islands. These islands are also considered to be the remnant of a former considerable extent of land which for a time was connected with a land mass extending from north to south along what is now the west coast of both Americas, but at some distance out in the Pacific Ocean. This connection of North with South America is certainly necessary to explain a host of otherwise inexplicable distributions. Parts of the present territory of Central America are known to have been submerged up to comparatively recent geologic times. Baur's pioneer theories regarding the Galapagos Islands here receive the appreciation which they have always so richly deserved. They are corroborated by evidence recently accumulated, all of which is used by Scharff to fine advantage. After some discussion favoring Scharff's theory, which presumes that there has been an extensive land mass occupying a considerable part of what is now the Pacific Ocean west of the present land areas, the author passes to a discussion of the South American fauna, which fills the rest of the book. (Chapters XIII–XV, pp. 336–435.) In this the views of von Ihering and Ameghino carry special weight, and to this they are certainly fully entitled.

Every one has previously been inclined to belittle the splendid energy and self-sacrificing zeal which have stood back of Ameghino's sensational accounts of his discoveries. To any one who has known Ameghino and who has heard him give his own reasons for his conclusions and describe his own treasures, this kindly appreciation by Scharff will seem well merited. This does not, of course, mean that we must accept all of Ameghino's theories, especially those regarding the origin of man.

A review, in the true sense, of Scharff's book is impossible! Each page is replete with valuable data, well digested, and is pregnant with suggestion. All of the critics of Scharff's previous works will agree that they are certainly suggestive in the extreme, even if their postulates may not be accepted. It seems caviling indeed to conclude this notice with a list of little faults, yet they are very evident, some of them, and may be corrected easily in subsequent editions. Thus on page 20 we should have *Carabus nemoralis,* instead of *memoralis,* a species which is not confined to Nova Scotia, but which for years has been the commonest large Carabid about Boston and Cambridge. On page 141, dealing with the pine-barren flora and its northward prolongation, we find no mention of the most important contributions which have ever appeared regarding the relationship of the flora of Newfoundland with the coast regions further south, those of Merritt L. Fernald, while, besides, no mention is made of the writings of Witmer Stone or Harshberger, both well known in connection with their work on the pine barrens. Again on page 151 we are surprised to learn that raccoons breed well in confinement and also to find no mention of the species of *Procyon* described by Miller from the French West Indian Island of Guadeloupe. The knowledge of this fact would have been of great interest in connection with the occurrence of *Procyon maynardi* on New Providence, which Scharff admits is an enigma, and the other remarks on the dispersal of raccoons. On page 173 we read north Carolina, elsewhere correctly North Carolina. On page 180 we find *Crocodilus americanus* spoken of as the only West Indian species in the genus, the important *Crocodilus rhombifer* being passed by. On page 204 no mention is made of Boulenger's discovery of *Bombina maxima* from Yunnan, a fact which is most important, fulfilling the prediction made by Stejneger that a discoglossoid toad would be found in this area, the center of dispersal of the group. On page 266 we find Portorico, one word; on the map it is given correctly as Puerto

Rico. On page 281 *Saurecia* and *Panolopus* are mentioned; the former is hardly entitled to generic rank, a fact important in this connection, while the genus *Panolopus* Cope has been shown by Garman to have been based upon a specimen artificially mutilated. On page 282, in speaking of *Capromys* no mention is made of *C. ingrahamii*, a peculiar species long known from one of the Plana Cays in the southern Bahamas. On page 289 Toditæ should read Todidæ, while on page 291 it would have been worth while mentioning the fact that de la Torre, of Havana, has published the account of finding fossil ammonites of Jurassic age in the Sierra de Vinales, western Cuba. Such trifling errors and omissions do little to mar the book! Its general excellence carries it far beyond petty criticisms. While the views which Scharff expresses will doubtless meet with opposition from many naturalists of the "old school," nevertheless they represent those which have been gaining ground fast and which will in time be held by all zoogeographers. As James Bryce's "American Commonwealth" came from England, so indeed does Scharff's American Animals coming from Ireland stand as by far the most important contribution to a knowledge of the subject it discusses. Indeed, it is likely to remain so for many a long day.

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